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FLORAL MORPHOLOGY  
*A NEW OUTLOOK*





# FLORAL MORPHOLOGY

A NEW OUTLOOK

with special reference  
to the  
Interpretation of the Gynæceum

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VOLUME TWO

WITH ADDITIONAL ILLUSTRATIONS AND INDEX  
FOR VOLUME I

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## PREFACE

The genesis and scope of the book of which the present is the second and concluding Volume have been indicated in the Preface to Volume I, which appeared in April, 1937.

In this earlier Volume certain general principles underlying floral construction, in particular those governing the radial relations of the several whorls of floral members, are outlined in a brief Introduction (Part 1). The application of these principles is illustrated in the succeeding descriptions of 39 Families selected as presenting various problems in floral construction. With this outlook as the key-note these Families were chosen irrespective of their systematic position, though so far as was compatible with this plan those more closely related were grouped together in sections (Parts 2-4). One or more Types were cited in each Family as being particularly suitable for examination and illustration of the principles laid down and as being at the same time likely in general to be more or less easily procurable.

The same scheme has been followed in dealing with the 151 additional Families (Families 40-190) treated in the present Volume (Parts 5-16). Since, however, many of these Families present problems already considered in detail in Volume I it was possible to follow a more natural division in the grouping. It will be obvious that the above total does not exhaust the full list of Families recognised to-day. But it appeared inadvisable, merely for the purpose of making this list complete, to increase further the size of the present Volume by the inclusion of Families which would mainly involve a repetition of the considerations already set forth, or others containing very few genera to which reference will be found in the literature cited, *viz.* Eucryphiaceæ (7, p. 616, Figs. 205, 206), Turneraceæ (16, pp. 91, 92, Figs. 36-42, and Diagram 4),

Malesherbiaceæ (16, p. 93, Fig. 43, and Diagram 6), Rafflesiaceæ (Cytineæ) (16, pp. 108-113, Figs. 60-71, and Diagrams 10, 11), Taccaceæ (16, pp. 115, 116, Figs. 83-90), Stachyuraceæ (23, pp. 683-685, Figs. 132-139, and 28, p. 297), Rapateaceæ and Myacaceæ (28, pp. 311, 312, Figs. 13-15).

The text is illustrated with 42 Figures (Figs. 7-48). Figs. 7-38 illustrate Families included in the present Volume. Figs. 39-48 relate to genera contained in Families which have been treated in Volume I. These latter Figures have been introduced to give examples from sections of flowers of the relation of the vascular scheme to the floral ground-plan, or to exhibit some fundamental feature of the gynæceum in genera not illustrated by Figures in the original accounts to which reference is made under their respective Families in Volume I. They include, also, specimen floral diagrams illustrating the modification required in the traditional diagrams in common use to bring them into line with the recent additions to our knowledge. These diagrams appeared originally in the papers listed in the Introduction to Volume I (pp. 23-25), and are reproduced here (some after improvement) by courtesy of the editors of the publications cited. For convenience of reference this list is reprinted with some additions (31-34) in the present Volume (p. 135). As in Volume I reference to these papers in the text is indicated by a corresponding number enclosed in brackets, followed by the sign † when the original paper is illustrated with figures and by the sign ‡ when it contains floral diagrams.

An asterisk prefixed to a name indicates that the species occurs in the British Isles or that the genus is represented in the British Flora.

Pages, Parts, Families and Figures are numbered consecutively after those in Volume I.

The separate Appendix has been included in the Volume as having a definite historical interest in view of the interpretation of the gynæceum founded upon new evidence which has been outlined in the present work. It contains a reproduction of an exhibit by the author at the meeting of the British Association for the Advancement of Science, held at Cambridge in August, 1938. The purpose of the exhibit was to present, by means of citation and comment, an epitomised historical survey of the challenge to the traditional view of the structural nature of the gynæceum contained in the writings of numerous botanists between 1823 and 1923.

E. R. SAUNDERS.

*Cambridge, January, 1939.*

## Volume I

### ERRATA

- P. 94. *For* Figure 5 *read* Figure 6.  
 P. 97. *For* 39. Juncaceæ *read* 39. Cyperaceæ.

### ADDENDA

- P. 36, par. 2, l. 1. *After* \**Clematis*. *insert* (19b, p. 210, Figs. 13A, 13B, 14A, 14B).  
 P. 114, l. 16. *After* foot-note 1 *insert* and 19a, 19b†.  
 P. 118, par. 2, l. 1. *After* 104-106† *insert* and 19b, p. 204, Fig. 9.  
 P. 118, par. 6, l. 3. *After* Fig. 31 *insert* and 19b, p. 204, Fig. 8.  
 P. 128, l. 2 from the bottom. *After* (Pitcher Plant) *insert* (19b, p. 210, Figs. 12A, 12B).



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## INTRODUCTION

Certain new and important general principles underlying floral construction have been treated in the Introduction to Volume I. It is therefore unnecessary to devote space in the present Volume to any general consideration of floral anatomy. Since, however, the relation of the vascular ground-plan to the floral ground-plan has not hitherto been fully recognised, and in view of a certain misconception which has from time to time found expression, it may be well to emphasise the fundamental feature underlying these relations. In the typical and simplest case a single vascular bundle turns out from the central cylinder of the axis and after traversing the cortical tissue of the axis to the exsertion level is continued into the corresponding floral member as the midrib of that member. If the floral member is of dorsiventral form and has a not inconsiderable lateral dimension this bundle almost always gives rise sooner or later to a pair of primary laterals. Additional pinnate branching may or may not follow later. Palmate branching is rare and is probably confined to types in which this form of branching characterises the foliage leaves. If this primary pair of laterals develops between the point of departure of the main bundle from the central cylinder and the exsertion level three bundles will enter the base of the floral member. But if, as more frequently happens, the main bundle remains unbranched during its course to the exsertion level and forms the first pair of laterals above this level, the floral member, whether sepal, petal or valve type of carpel will be furnished at its base with only one bundle, the midrib.

It may then be said that the fundamental feature of the whole vascular scheme is the departure from the central axial cylinder of bundles corresponding in number and in their radial disposition with the number and arrangement of the floral members. This concordance may, however,

in some types become obscured or modified by fusions owing to stringency of space conditions; by a complex breaking-up of the vascular units composing the central cylinder into a large number of small strands before the departure of the bundles for the floral members; or by absence of certain bundles through degeneration and final loss. That the number of bundles in a floral member at the exertion level happens in some types to be three does not indicate a basic feature of the scheme. The primary laterals can arise at any point above this level as well as below. Hence the presence of *three* bundles at the base of any particular set of dorsiventral floral members has no more significance than that of indicating a low level of branching of the midrib bundles of a particular whorl in particular species or genera. On the other hand the main bundle of floral members of cylindrical form commonly remains unbranched as almost invariably, for example, in stamens. But if the staminal filament is considerably extended laterally, even though bearing a normal fertile anther, the main bundle may give rise to a branch system as in certain genera of the Campanulaceæ. Or if a carpel of solid (cylindrical) form in the lower region of the ovary becomes laterally extended above, the main bundle, unbranched below, may undergo branching at the higher level. Or, again, if the stamens become sterile and assume a typical foliar form the main bundle may branch as in dorsiventral members of other whorls. In short, the formation of whorls of midrib bundles and their correspondence with the whorls of floral members is a fundamental feature of floral construction and the fact that these midrib bundles originate on definite radii provides a means of determining the number of members in a whorl. But whether, or at what level, these bundles branch has no significance in regard to the number of members in a whorl. Only their morphological form is thereby revealed.

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## Part 5

### Dicotyledons

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„	42.	Saxifragaceæ
„	43.	Pittosporaceæ
„	44.	Hamamelidaceæ
„	45.	Platanaceæ
„	46.	Rosaceæ
„	47.	Connaraceæ
„	48.	Leguminosæ



## 40. CRASSULACEÆ

Flower generally ♂, actinomorphic, six-whorled, pentamerous throughout (K 5 C 5 A 5 + 5 G 5, sterile + 5, fertile) (28, pp. 306, 307†) and obdiplostemonous. Rarely unisexual. Sometimes with 2-4 or 6-∞ members in the whorls; or five-whorled through suppression of the antepetalous stamen whorl. Outer, sterile carpels and loculi antepetalous in both five-whorled and six-whorled types. A whorl of hypocarpellary scales almost always present between the andrœcium and gynœceum on the radii of the sterile carpels. Gynœceum becoming more or less pseudo-apocarpous through median radial splitting of the fertile carpels from without inwards. Styles distinct. Fruit generally in the form of follicles, each of  $\frac{1}{2}$   $\times$   $\frac{1}{2}$  carpels, dehiscing down the ventral suture.

Sepals generally with commissural marginal veins. The constant position of the sterile carpels and loculi whether the flower is five-whorled or six-whorled follows from the vascular ground-plan. On the sepal radii the sepal midrib bundles arise independently. These are followed by a single set of trunk cords which furnish the antesealous stamen bundles and fertile carpel bundles. But on the petal radii the sepal commissural marginal veins, petal midrib bundles, antepetalous stamen bundles (when present) and sterile carpel midrib bundles are all derived from one set of trunk cords, hence the suppression of the antepetalous stamens will not affect the position of the succeeding carpel whorl. Obdiplostemony naturally accompanies this vascular scheme.

### ILLUSTRATIVE TYPES

**Sedum spp.** (Stonecrop) (28, Figs. 1, 2). K 5 C 5 A 5 + 5 (exceptionally, in a few species forming the section *Procrassula* A 5 + 0) G 5, sterile + 5, fertile. Petals free.

**Cotyledon Umbilicus** (Pennywort, Navelwort). Flower as in *Sedum* (see above), but corolla tubular.

**Crassula spp.** K 5 C 5 A 5 + 0 G 5, sterile + 5, fertile (28, Figs. 3, 4).

**Sempervivum tectorum** (Houseleek). K  $n$  C  $n$  A  $n$  +  $n$  G  $n$ , sterile +  $n$ , fertile,  $n$  varying between 6 and 20.

## 41. CEPHALOTACEÆ

Flower ♂, actinomorphic, four-whorled through absence of a separate corolla whorl and of a second carpel whorl, hexamerous, diplostemonous (T 6 A 6 + 6 G 6) (28, pp. 299, 300). Tepals with white marginal strips. Gynæceum apocarpous. Ovules generally solitary. Individual fruits one-seeded.

Tepals with commissural marginal veins. In types with a single perianth and two stamen whorls the presence of tepal marginal veins of commissural origin with which the alternit tepalous stamen bundles are at first conjoined is characteristic. For this construction makes it possible for a staminal whorl to be the outermost whorl on these radii, a ground-plan which probably does not occur in isomerous types except under these conditions. The same relations are illustrated in *Chrysosplenium* (see later in the present Volume under Saxifragaceæ, Part 5, p. 156) and doubtless in *Colobanthus Billardieri* (Caryophyllaceæ). In such types the tepals are never wholly green, but are coloured (*i.e.* are non-green) or white along the edges or over the whole inner surface. Thus, though a separate corolla is not present, the corresponding sectors have a petaloid character (see Vol. I, Introduction, pp. 9, 10; and *Thomasia* (Sterculiaceæ), Part 4, p. 118; also 19a, 19b).

## ILLUSTRATIVE TYPES

**Cephalotus follicularis.** A West Australian Pitcher plant. See the characters of the Family.

## 42. SAXIFRAGACEÆ

Flower generally ♂, more or less perigynous or syngonous, actinomorphic. Exceptionally, unisexual through abortion; or almost hypogynous; or zygomorphic; or with a reduced number of whorls through absence of the corolla (e.g. *Chrysosplenium*), or of the antesepalous stamens (e.g. some species of *Mitella*), or of the antepetalous stamens (e.g. *Ribes*, *Heuchera*, *Escallonia*, *Itea*, other species of *Mitella*). Gynæceum sometimes isomerous with the outer whorls and with an equal number of sterile and fertile carpels (*Francoa*, *Philadelphus*, *Carpenteria*, *Dein-anthe*); sometimes oligomerous and with an equal number of sterile and fertile carpels (*Parnassia*, *Hydrangea*, *Deutzia*, species of *Saxifraga*, *Ribes*); sometimes with more carpels sterile than fertile (species of *Saxifraga*, *Heuchera*, *Tellima*, *Itea*, *Escallonia*, *Chrysosplenium*); in perigynous and partially syngonous types generally becoming pseudo-apocarpous. Stamens in a few genera  $> 10$ , either through multiplication of the antesepalous whorl (e.g. *Philadelphus*) or of both whorls (e.g. *Hydrangea*). Ovary bi- to multilocular, often becoming unilocular above as the fertile carpels cease to reach the centre; or unilocular throughout. Sometimes crowned with a disc (*Deutzia*, *Escallonia*, *Philadelphus*). Styles seldom connate, more often two or more as the result of median radial splitting of the fertile carpels. When more than one they vary in composition from  $\frac{1}{2} \text{ } 1 \frac{1}{2}$  carpels in types in which alternate carpels bear ovules to  $\frac{1}{2} \text{ } 4 \frac{1}{2}$  carpels in types in which the number of actually (as opposed to potentially) fertile members is reduced to two without reduction of the total number (10). The group of sterile carpels in each half of the ovary together with half of each fertile carpel is then moulded into a single style filament (e.g. *Tellima grandiflora*). Ovules generally in several, rarely only in

two rows. Fruit in types in which the gynæceum becomes pseudo-apocarpous of two or more folliculoid partial fruits; in syncarpous types generally a capsule, sometimes a berry.

Sepals and tepals generally with commissural marginal veins, the tepals being then partly or wholly non-green (see below under *Chrysosplenium* among Illustrative Types and Vol. I, Introduction, p. 10; also 19a and 19b).

In no member of the Family do the vascular bundles for every whorl originate independently. In most syngonous types the midribs for all the whorls are derived from a single trunk cord on each radius. If such types are six-whorled and primarily isomerous, with a multilocular ovary in which half the total number of carpels are fertile, the loculi are antesealous, the andrœcium diplostemonous and the stigmas centred over the sterile carpels (e.g. *Deutzia* when double-flowered). In a few perigynous types the bundles for some whorls arise independently and for the others are combined in trunk cords. If such types are six-whorled and isomerous throughout and have a multilocular ovary in which half the total number of carpels are fertile, the vascular fusions are such that the loculi are antepetalous, the andrœcium obdiplostemonous and the stigmas centred over the fertile carpels ('commissural') (see *Francoa* under Illustrative Types; also 28, p. 308). In some perigynous types with an oligomerous gynæceum the carpel bundles originate independently. In such types the transition from the fuller ground-plan of the outer whorls to the reduced ground-plan of the gynæceum is preceded by a process of reconstruction in the central vascular cylinder. In this way equal spacing of the reduced number of members is effected, some of the outer carpel midribs being formed on perianth-andrœcium radii and some on new radii (see *Parnassia* under Illustrative Types; also 16, pp. 113, 114). Where, as is much more frequently the case in this Family, the carpel midribs are carried out as components of the trunk cords which also furnish the perianth and andrœcium bundles, and where consequently no process of reconstruction precedes their formation it is obvious that equal spacing of the carpels will be impracticable in types with a pentamerous perianth and andrœcium and a reduced number of carpels (8, 6 or 4). This inevitable asymmetry is minimised by the abandonment of the restriction of sterile and fertile carpels to different sets of radii. The several bundles for each class of carpel are then derived from trunk cords, some of which

lie on sepal radii and some on petal radii (see *Saxifraga* and *Ribes* among others under Illustrative Types).

The occurrence within the Saxifragaceæ of some types showing the full proportion of fertile carpels (*i.e.* half the total number) as in *Francoa* and of other types with only the minimum number compatible with isobilateral symmetry (*i.e.* two) is paralleled in Papaveraceæ (see under that Family in Vol. I, Part 2, p. 45). Such a type as *Francoa* (see below under Illustrative Types) may be compared with a few-carpelled genus such as *Meconopsis*, while the same reduction in fertility which characterises *Saxifraga*, *Tellima*, *Ribes* and numerous other genera (see below under Illustrative Types) is found in *Eschscholzia* (*loc. cit.*, pp. 49–52). In the latter genus there is the same centring over a group of sterile carpels of the two styles commonly formed in the later flowers in place of the four always present in some earlier flowers. The resemblance between the first-mentioned representatives of the two Families extends further. For in both *Francoa* and *Meconopsis* the sessile stigmas are 'commissural,' and dehiscence of the fruit takes place by the separation of the carpel tips (see *Francoa* among Illustrative Types). On the other hand *Eschscholzia* differs from *Saxifraga* and allied genera in the manner of dehiscence of the fruit. In *Eschscholzia* the fertile carpels split away whole from the intervening groups of sterile carpels. In the perigynous genera *Saxifraga* and *Tellima* and similar forms the two opposite fertile carpels split in half. Each of the two resulting partial fruits in those species with G 6–10 in which only two are fertile consists of a group of sterile carpels flanked on each side by half of each fertile carpel (see *Saxifraga* and *Tellima* among Illustrative Types).

In the above account the various forms of saxifragaceous gynæceum are interpreted as being for the most part derived from an isomerous ground-plan which in many genera has become modified as the result of restriction of space and loss of fertility. But although this interpretation brings the different types of construction satisfactorily into line it should be added that in some species the mode of origin of the placental bundles shows a departure from the usual arrangement in which these bundles are given off directly from the corresponding carpel midribs. In the species in question in which the ovary is generally bilocular, the elements which furnish the placental bundles are left behind in the centre as the trunk cords for the several whorls begin to turn outwards below the level of the loculi. They are not confined to particular radii but may be scattered in a ring or consolidated into a central core, which at a higher level becomes organised into the (generally) two placental bundles. These two



bundles and the corresponding septa may then stand in line (in accord with expectation) with two opposite trunk cords. Or one of the pair may occupy such a position but the other may be aligned on an opposite radius *between* two trunk cords. Or both bundles may be thus aligned. These variations which are probably attributable to irregular combinations and consequent eventual unequal spacing of trunk cords are without significance in respect of the floral ground-plan. For (1) these differences in alignment of the placental bundles can occur in different flowers on the same individual. And (2) in types with a unilocular ovary in which the placental bundles are formed above the level of origin of the locus they are detached from individual and opposite trunk cords as in *Ribes*, *Heuchera* and *Tiarella*. It may be concluded that the unusual mode of origin of the placental bundles described above is merely incidental to the speeding-up which leads to their delimitation at an exceptionally early stage.

### ILLUSTRATIVE TYPES

(a) Gynæceum isomerous with the outer whorls. Fertile carpels equal in number to the sterile carpels.

**Philadelphus coronarius** (Syringa). Flower syngonous, isomerous, predominantly tetramerous but not infrequently pentamerous, five-whorled owing to suppression of the antepetalous stamen whorl but, nevertheless, with numerous stamens owing to multiplication of the antesepalous members (K 4 or 5, with commissural marginal veins, valvate C 4 or 5 A  $4_x + 0$  or  $5_x + 0$  G 4 or 5, sterile, antepetalous + 4 or 5, fertile, antesepalous). Ovary crowned by the carpellary disc, multilocular below where the fertile carpels are fused in the centre, becoming unilocular above as these carpels become defined and free on their inner face though remaining in contact. Carpellary disc with differentiated vascular strands. Styles united into a single filament below, separating above into the stigmatic arms which stand in line with the sterile carpels and loculi. Each of the 4 or 5 component style filaments receives the whole vascular system of a sterile carpel and half that of the adjacent fertile carpel on each

side and corresponds to  $\frac{1}{2} \times 1 \frac{1}{2}$  carpels. Fruit a capsule, dehiscing loculicidally through splitting in the mid-line of the sterile carpels.

As in general in the syngonous types the midrib bundles for the several members on each radius are derived from a single trunk cord.

**Francoa** (28, p. 308). Flower very slightly perigynous, tetramerous, six-whorled (K 4, with commissural marginal veins C 4 A 4 + 4, obdiplostemonous G 4, sterile, antepetalous + 4, fertile, antesepalous). Sepals exserted from the sides, petals from the angles of the four-sided axis. Eight non-vascular disc structures alternate with the eight stamens. Ovary almost free becoming pseudo-apocarpous through median radial splitting of the fertile carpels, quadrilocular, becoming unilocular above as the central parenchyma comes to an end and the fertile carpels fail to reach the centre. Stigmas sessile, standing over, and derived from, the fertile carpels ('commissural'). Fruit a capsule, opening at the apex through separation of the tips of the sterile carpels from the fertile carpels after the sterile midribs have come to an end.

The antesepalous stamen bundles originate from the central cylinder very close to the sepal midrib bundles but are probably distinct. But whether they are or are not, in fact, organised from the same vascular units as the latter bundles, obdiplostemony and antepetalous loculi are here brought about independently of this relation. For petal midrib, antepetalous stamen, and sterile carpel bundles arise conjoined into a single set of trunk cords. These cords lie on the longer radii (*i.e.* those in line with the angles of the axis). With more space available on these than on the alternate (antesepalous) radii the antepetalous stamen bundles are carried by the corresponding trunk cords further from the centre than the antesepalous stamen bundles before these cords are resolved into their components. Antepetalous loculi then naturally follow.

(b) Gynæceum oligomerous through reconstruction. Fertile carpels equal in number to the sterile carpels.

**\*Parnassia palustris** (Grass of Parnassus) (16, pp. 113, 114). Flower very slightly perigynous, with isomerous outer whorls but with a reduced gynæceum, six-whorled (K 5, with true lateral veins C 5 A 5 + 5 (staminodes) G 4, sterile + 4, fertile). The antesepalous stamen bundles do not arise, as in the syngonous types, as components of trunk cords but turn out from the central cylinder independently; the antepetalous staminodes are non-vascular. The transition from the pentamerous vascular ground-plan of the outer whorls to the tetramerous ground-plan of the gynæceum is brought about by a process of reconstruction in the central cylinder. In this way the sterile carpel midrib bundles which, like the antepetalous stamen bundles originate independently, can be equally spaced. One of these midrib bundles turns outwards on a sepal radius, one on the opposite petal radius, and the other two on new, intervening radii. Ovary syncarpous, almost free, without disc, quadrilocular below, becoming unilocular above as the fertile carpels cease to reach the centre. Stigmas derived from, and standing over, the fertile members ('commissural'). Fruit a capsule, opening above by separation of the tips of the fertile carpels above the level at which the shorter sterile members come to an end.

(c) Gynæceum oligomerous through suppression. Fertile carpels equal in number to the sterile carpels.

**Hydrangea spp.** Inflorescence with the peripheral flowers generally sterile.

Sterile flower. K 4 (or 5 or 3), large and petaloid, with commissural marginal veins. Sepals, when 3, with convolute præfloration (each overlapping one of its neighbours and being overlapped by the other). When 5, quincuncially arranged (see Fig. 7).

[In the quincuncial arrangement the several numbers of the whorl have an angular divergence of  $2/5$  and lie on a

continuous spiral, the overlap of their respective edges occurring as follows : sepals 1 and 2 have both edges outside their neighbours ; sepal 3 has one edge outside and one edge overlapped by sepal 1 ; sepal 4 is overlapped by sepals 1 and 2, and sepal 5 is similarly overlapped by sepals 2 and 3.]

Sepals when 4 in two pairs, one outer, one inner, as commonly is the arrangement of sepals or tepals in tetramerous types as *e.g.* in Cruciferae and Nepenthaceae (see under these Families in Vol. I, Part 2, p. 41, and Part 4, p. 128, respectively), and in the present Volume,

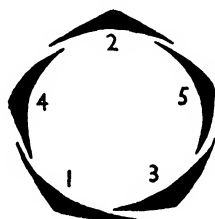


Diagram of the quinuncial arrangement in the usual case in which sepal 2 lies at the back. The direction of the spiral is shown as clockwise. For an anti-clockwise spiral see p. 206, Fig. 9.

FIGURE 7.

under *Rivina*, Part 10, p. 370, Tamaricaceae, Part 7, p. 247, Urticaceae, Part 9, p. 338, Lauraceae, Part 10, p. 383, Ericaceae and Sapotaceae, Part 11, pp. 394 and 415, respectively. But here, as elsewhere, the two pairs together behave as, and are equivalent to, a single whorl. C, A and G more or less reduced or aborted.

Fertile flower syngonous. K 5 or 4, small, with true lateral veins C 5 or 4  $A > 8$  or  $> 10$  owing to irregular multiplication of both whorls. G (through suppression) generally 4, sometimes 6 or 8 (*e.g.* *H. petiolaris*). Ovary bi-, tri-, or quadrilocular at the extreme base but immediately becoming unilocular. Free summit of the ovary glandular but no separate well-defined disc. Styles distinct, 2-4, equal in number to the sterile carpels and

centred over these carpels. Each style receives a sterile carpel midrib and half the vascular system of the neighbouring fertile carpel on each side and thus corresponds to  $\frac{1}{2} + \frac{1}{2}$  carpels. The three bundles shortly fuse into a single strand which below the stigma level divides in two. It may be inferred that these two strands belong to the two half carpels and that the bundle of the intervening whole sterile carpel has come to an end at a lower level. This would account for the slightly bilobed form of the stigma, not an uncommon feature in other genera of the Family (see below under *Deutzia* and *Mitella*) for the sterile carpel midribs are here very generally less strongly developed than the bundles of the fertile members, a difference in vigour sometimes further emphasised by an accompanying difference in carpel length (see above under *Parnassia*).

As in general in the syngonous types, the midrib bundles for the several members on each radius are derived from a single trunk cord, but the elements which give rise to the placental strands of the fertile carpels are delimited from the central cylinder before these cords have left the centre. Some of the trunk cords turn out singly on their proper radii; others, owing to restriction of space, arise two or three together and diverge sooner or later to take up their proper positions. Consequently the derivation of the placental strands from particular cords is not obvious. But the arrangement of the fertile carpels (indicated by the position of the placental cushions) is in general as symmetrical as the numerical relations of the whorls permit. This relation may, however, be disturbed by the above-mentioned unequal spacing of the trunk cords at the level of origin. Thus, if a flower with a pentamerous perianth has a gynæceum with two fertile carpels, these carpels (= the septa) may stand in line with two opposite vascular units at the flower base. But in some flowers these units will be composed of two or three trunk cords which, when they separate, will diverge and occupy their proper radii. It may then result that above this level, the ovary being now unilocular, the two placental cushions no longer stand in line with opposite trunk cords. It is evident that when three or four fertile carpels are present in a flower with a pentamerous perianth, their distribution in relation

to the ten trunk cords, even apart from such disturbance, can only be approximately symmetrical, since the number of trunk cords intervening between them must vary. It follows from the nature of the vascular relations that a completely, or even an approximately symmetrical, ground-plan involves the abandonment of the usual restriction of sterile and fertile carpels to different sets of radii. This means that the potentiality of the carpel component of individual trunk cords is not rigidly fixed. In one flower this component of a particular trunk cord may become the bundle of a sterile member and in another this component of the corresponding cord may serve a fertile member.

**Deutzia spp.** K 5 C 5 A 5 + 5 G generally 6 or 8 of which half are sterile and half fertile. The general construction of the flower is similar to that of *Hydrangea*, but it differs in the following features. (1) The ovary is trilocular or quadrilocular almost throughout, only becoming unilocular near the summit. (2) The disc is well-developed, in part roofing-in the ovary and in part lining the base of the perianth-andræcium wall, and possesses a network of differentiated vascular strands derived from all ten trunk cords. Stigmas deeply bilobed, owing presumably to the same cause as in *Hydrangea* (see above). Also, as in *Hydrangea*, the two kinds of carpels are as equally spaced as the numerical combinations allow and consequently are not restricted to different sets of radii.

In a double-flowered form in which the stamens are replaced by  $\infty$  petaloid structures, the gynæceum, in contrast with that of the single type, is generally isomerous with the outer whorls (G 5, sterile + 5, fertile). As in the oligomerous gynæceum of the single type, sterile and fertile carpels alternate. But in the double form the two kinds of carpels, as in all isomerous types, are restricted to the different sets of radii, the sterile carpels being all antesepalous, the fertile all antepetalous. Occasional flowers of this variety serve excellently to illustrate the connection between stringency in the spatial conditions and reduction in fertility. In these exceptional flowers, the ovary, though composed of 5 sterile and 5 fertile carpels, is quadrilocular, one loculus being much larger than the other three. The three normal-sized loculi stand in line

with three of the five antesepalous trunk cords which furnish the sterile carpel bundles. The four partitions corresponding with four of the usual five fertile carpels stand in line with four of the antepetalous trunk cords. The large loculus occupies the three remaining radii, *i.e.* it stands in front of the fifth antepetalous trunk cord and of each of the neighbouring antesepalous cords. This configuration results from the fact that the fifth fertile carpel standing in line with the middle (antepetalous) cord of the above-mentioned triplet behaves in the lower region of the ovary as a sterile carpel. It does not project inwards to form a partition, hence the large double-sized loculus. Only at a level at which the four other fertile carpels have almost ceased to produce ovules does this fifth antepetalous member begin to extend inwards towards the centre as an incomplete partition, and to bear ovules which now find room in the space vacated at this level by the ovules of the adjacent fertile carpels (unpublished). In a flower in which the spatial conditions were slightly more stringent this fifth antepetalous carpel would, presumably, become entirely sterile. No placental cushion would be formed on this radius. The carpel would apparently have disappeared. Flowers showing a similar apparent disparity in the number of sterile carpels, fertile carpels, and loculi occur occasionally in many isomerous types in which the two kinds of carpels are restricted to alternating radii, *e.g.* *Rhododendron racemosum*, *Aristolochia Pistolochia*, *Styrax sp.*, while in *Castanea vulgaris* withdrawal from the centre in the upper part of the ovary of one or more fertile carpels, which below formed complete septa, is so general as to become the rule rather than the exception (see under Fagaceæ later in the present Volume, Part 9, p. 332). In the above cases the fertile carpels and loculi appear at some levels to be one or more fewer than the sterile carpels, one or more loculi being, however, of double size. Less often stringency of spatial conditions may lead to the development of two neighbouring septa-forming fertile carpels so near together that although a sterile carpel is present on the intervening radius, as shown by the presence of a corresponding midrib bundle, no loculus makes its appearance in line with this latter carpel. (For such a construction in an exceptional flower of *Chaenomeles Lagenaria* (*Cydonia japonica*) see 5, p. 216, Fig. 23 and p. 221.) In these circumstances a similar apparent disparity is produced, not by the formation of a double-sized loculus through the apparent disappearance of a fertile carpel, but through the formation of a double-sized septum through the apparent disappearance of a sterile carpel.

(d) Gynæceum oligomerous through suppression. Fertile carpels ordinarily reduced to 2, only very rarely with as many as 3-5. Sterile carpels 2 or more, but rarely as many as 8.

**\*Saxifraga.** Flower more or less perigynous, almost always actinomorphic (for the symmetry of the gynæceum see below), pentamerous in the outer whorls (K 5, with commissural marginal veins C 5 A 5 + 5). Gynæceum ordinarily with two carpels fertile (indicated by the number of placentæ and placental bundles) and two or more, but rarely as many as eight, carpels sterile (indicated by the number of trunk cords which give rise to carpellary bundles, or, in other words, by the number of construction radii on which these bundles originate). Ovary bilocular below becoming unilocular above as the fertile carpels which stand opposite to one another fail to meet in the centre, shortly becoming pseudo-apocarpous through median radial splitting of the fertile carpels. Styles two, formed from all the carpels, centred over the one or more sterile carpels intervening between the fertile members. Stigmas terminal.

A few species and some hybrids produce one or two flowers, occasionally or constantly, with pentamerous outer whorls but with three styles or even four or five. For example, three-styled flowers predominate in *S. florulenta*, the minority being two-styled and four-styled. Three-styled terminal flowers occur exceptionally in the species *stellaris*, *magellanica*, *aizoides*, *kumaunensis* and even five-styled flowers have been recorded in *punctata*, *Lyallii*, *stellata* and *kumaunensis*.

These exceptional instances of fuller development indicate that the original ground-plan of the gynæceum in *Saxifraga* is G 5, sterile + 5, fertile (a construction common in the early flowers of *Philadelphus*, see above, p. 143), and that through sterilisation the number of fertile carpels in the bulk of the flowers of all but a few species has now come to be only 2. In such a form as *Hydrangea petiolaris* (see above, p. 149), in which flowers with 4, 3 and 2 fertile carpels often occur irregularly in the same inflorescence this process of sterilisation is still in course of taking place. This species has not yet




reached, throughout its development, the end stage, *viz.* that condition of stability represented by the maximum degree of sterilisation compatible with some degree of fertility and with isobilateral symmetry. In *Saxifraga* this condition has, with few exceptions, now become established. The trend towards reduced gynæceal fertility is widespread in the Family. In many genera it takes the form of a reduction in the number of carpels, of the sterile equally with the fertile (see above under *Parnassia*, *Hydrangea*, *Deutzia*). In *Saxifraga* reduction in the total number of carpels has not marched with the decline in fertility but has proceeded at a slower rate. Within the genus are some species showing the maximum of reduction and of sterilisation ( $G = 2$ , sterile + 2, fertile); others also showing the maximum of sterilisation but accompanied by less reduction in number ( $G > 2$ , sterile + 2, fertile); and yet a few others in which the sterilisation process has begun but is variable in degree (see the species cited above), and is not in all cases accompanied by reduction in number ( $G > 5$ , sterile +  $> 2$ , fertile). [*N.B.* The sign + is not used here to indicate a corresponding distribution in whorls but merely in the simple sense of addition.]

The median radial splitting of the fertile carpels is accompanied by the inrolling of the edges thus produced, so that when there are two such carpels each edge of the one split carpel comes into contact, though it remains unfused with the opposed edge of the other split carpel. Thus each half of the ovary tapers into a separate style centred over the one or more sterile carpels intervening between the fertile members.

In some species some of the ten trunk cords from which the bundles for the several whorls are derived may remain fused for a considerable distance before they separate. In many, two or three cords arise very close together in line with one of the placentæ. Or such a group may arise opposite each of the two placentæ. This distribution renders it difficult to trace the derivation of the placental bundles to particular trunk cords, but the appearance at a higher level accords with the construction described above. In neither half of the gynæceum does any sterile carpel bundle occupy the position corresponding to the lateral mid-line since this mid-line does not coincide with any of the ten construction radii. For a plane at right angles to the plane in which the two fertile carpels lie will pass between sterile carpels so that two of these

carpels lie on each side of it in each half of the gynæceum. But there is a tendency for one of these standing next to this line to shift into this position. As a result of this asymmetrical conformation, possibly accentuated by the above-mentioned common point of origin and consequent final irregular spacing of some trunk cords, the two halves of the gynæceum face one another slightly askew, and in species having long and slender styles the free ends of the styles may become crossed like the ill-adjusted legs of a pair of tongs.

**Tellima grandiflora.** Flower slightly perigynous, with the ground-plan of species of *Saxifraga* but having an ovary unilocular throughout. The following features are particularly easily observed. (1) The median radial splitting of the fertile carpels, since this results here in the opening of the loculus to the exterior already in the flowering stage. (2) The derivation of the vascular system of the whole gynæceum from the ten primary trunk cords and at a higher level the division of the two fertile cords. For owing to the membranous nature of the ovary wall, which is free from the perianth-stamen wall almost to the base, it is easily rendered transparent, thus allowing the course of the vascular bundles to be followed in the intact structure. (3) The slightly skew 'set' of the two styles. This is manifest on inspection of the two rather large semicircular stigmas and in cross sections of the styles which in outline often resemble two letters C interlocked, thus .

**Heuchera spp.** Flower as in *Tellima* (see above) except that the antepetalous stamen whorl is suppressed. K 5 C 5 A 5 + 0 G 10 (8 sterile, 2 fertile), each half of the gynæceum of  $\frac{1}{2} \frac{1}{4} \frac{1}{2}$  carpels.

As the vascular bundles for all members on each radius are derived from a single trunk cord the suppression of the antepetalous stamen whorl does not affect the radial relations of the carpels.

**Tiarella spp.** (e.g. *T. cordifolia*, *T. trifoliata*). Flower similar in the main to that of *Tellima* (see above) but differing from all other genera in the Family in that the two free halves of the gynæceum are patently unequal in size. This inequality goes hand in hand with unequal spacing of the ten trunk cords which serve the several whorls. The two cords from which the fertile carpel bundles are derived originate separately, as also do six of the others. But the remaining two arise as one cord which lies next to one of those furnishing a fertile carpel bundle. When this compound cord becomes resolved into its two components they do not become as widely separated as those which originated independently. Hence when two halves of the gynæceum become free the half which includes

the originally conjoined pair of cords is always smaller than the other half.

***Itea virginica*.** Flower with the ground-plan of *Heuchera* (see above). K 5 C 5 A 5 + 0 G 10 or fewer by suppression (8 or fewer sterile, 2 fertile), but with a syncarpous bilocular ovary and a single style with a bilobed stigma.

*Itea* differs from the other types cited in this group in that the sterile carpel bundles are detached from the corresponding trunk cords at the level of origin of the loculi. As the ovary shortly becomes disjoined from the perianth-stamen wall and remains syncarpous it offers particularly favourable material for observation of the carpel bundles.

***Escallonia* spp.** Flower with the ground-plan of *Heuchera* (see above) K 5 C 5 A 5 + 0 G 10 or fewer by suppression (8 or fewer sterile, 2 fertile) but syngonous with a syncarpous ovary crowned by a large disc, and with a single style.

The carpel bundles, detached from the corresponding trunk cords at the level of the disc, are unusually strongly developed, as is also the network of veins in the disc.

**\**Chrysosplenium* spp.** (e.g. \**C. oppositifolium*). Flower syngonous and tetramerous. Corolla absent. T 4, greenish yellow A 4 + 4 G (probably) 8, 4 orthogonal, 4 diagonal; the two lateral carpels fertile, the two median and the four diagonal sterile. As in *Saxifraga* (see above) the vascular bundles for all structures on each radius are derived from a single trunk cord. The 4 cords on the tepal radii furnish the tepal midribs and the antetepalous stamen bundles and 2 lateral carpel bundles, no carpel bundles being detached from the 2 cords in the median plane; those on the alternitepalous radii the commissural marginal veins of the tepals which are therefore coloured (see Vol. I, Introduction, pp. 9, 10 and under *Thomasia* (Sterculiaceæ), Part 4, p. 118; also earlier in the present Volume under *Cephalotus* (Cephalotaceæ), Part 5, p. 142; also 19a and 19b), alternitepalous stamen bundles and carpel bundles. Gynæceum pseudo-apocarpous above through median radial splitting of the fertile carpels as the ovary becomes disjoined from the outer whorls. This splitting is anticipated by the forking of the placental

bundle of each fertile carpel in the basal region of the ovary and the divergence of the resulting twin strands. Styles 2, centred over the median sterile carpels. Each style filament receives (? always) four vascular strands, two representing half the vascular system of each of the two lateral fertile carpels and two the whole systems of the two alternitepalous carpels in the corresponding half of the gynæceum. No bundle enters either style in the median plane. But as it is highly improbable that a compound style (*i.e.* a style derived from more than one carpel) which is centred on the radius on which a carpel has been lost would terminate in an undivided stigma, the two lateral carpels may be presumed still to be present though they have lost their vascular bundles. Accordingly, each style may be taken to represent  $\frac{1}{2} 3 \frac{1}{2}$  carpels. In a tetramerous flower such as that of *Chrysosplenium*, since the two halves are identical, the two styles face towards the centre and hence towards each other more strictly than in pentamerous types.

**\*Ribes** (*e.g.* **\*R. grossularia**, Gooseberry, **\*R. rubrum**, Red Currant, **\*R. nigrum**, Black Currant). Flower syngonous. K 5, with commissural marginal veins C 5 A 5 + 0. G generally 4, 2 sterile, 2 fertile. Ovary unilocular from the outset or immediately becoming so, tapering upwards into two styles as in *Saxifraga* or into a single filament which sooner or later divides in two. Stigmas terminal.

The vascular bundles for all members on each radius are derived from a single trunk cord as in *Heuchera* (see above), hence the suppression of the antepetalous stamen whorl has no effect upon the radial relations of the carpels. In many species (*e.g.* *R. rubrum*) the delimitation of the placental bundles occurs after the appearance of the loculus and after ten trunk cords have become distinct, hence the derivation of these bundles from two opposite cords is easily observed. As in *Saxifraga* the two kinds of carpels are not restricted to different sets of radii.

**Mitella.** Flower perigynous (*e.g.* *M. diphylla*) or syngonous (*e.g.* *M. pentandra*). K 5 C (usually) 5 A 5 + 5 (*e.g.* *M. diphylla*), or A 5 + 0 (*e.g.* *M. trifida*), or A 0 + 5 (*e.g.* *M. pentandra*) G 4, 2 sterile, 2 fertile. Staminal filaments non-vascular. Even were staminal vascular bundles developed, the variations in the andrœcium would have no effect upon the radial position of the carpels, since the vascular bundles for all members on each radius are derived from a single trunk cord. The vascular system of the unilocular ovary is reduced to the four bundles of the two sterile and the two fertile carpels. The other six sterile carpel bundles have been lost as also (so far as appears) the corresponding carpels.

**Astilbe spp.** Flower as in *Mitella diphylla* (see above), but with a bilocular ovary. Division in two of the fertile carpels occurs unusually early, appearing first as an interstitial slit before the ovary has become disjoined from the perianth-andrœcium wall. This early splitting is rendered possible by the symmetrical spacing of the primary trunk cords from the outset, for all ten arise separately and hence come to lie at once on their proper radii.

## 43. PITTOSPORACEÆ

Flower ♂, actinomorphic, hypogynous, pentamerous but generally with an oligomerous gynæceum (K 5 C 5 A 5 G 2 (or 3-5), sterile + 2 (or 3-5), fertile). No separate disc present but the superficial tissue in the five-angled basal region of the ovary has the glandular character of disc tissue. Ovary generally either with 2 (or 3-5) loculi below, becoming unilocular above as the fertile carpels fail to reach the centre, or unilocular throughout. Style single, terminal. Stigma capitate. Ovules in two rows on the placentæ. Fruit a capsule, dehiscent loculicidally, or a berry and indehiscent.

The vascular system of the gynæceum is accompanied by a system of resin canals, the two systems running together throughout.

## ILLUSTRATIVE TYPES

**Pittosporum.** Stigma convex, when lobed the lobes centred over the fertile carpels ('commissural'). Fruit a capsule, dehiscent loculicidally.

**P. Tobira, P. crassifolium.** G 3, solid, sterile, with midrib bundles which persist to the top of the style + 3, semi-solid, fertile. Ovary unilocular throughout.

**P. undulatum, P. tenuifolium.** G 2, solid, sterile with midrib bundles which cease to be traceable below the level of the loculi + 2 semi-solid, fertile. Ovary bilocular at the base, becoming unilocular above.

*Pittosporum* affords an example of the rare condition in which the lateral boundaries of the carpels are defined by a radial tract of cells extending inwards from each sterile carpel midrib (or from the corresponding positions in the region where these bundles are no longer traceable) to the border of the loculus. These radial tracts (as they appear when seen in transverse sections) extend vertically

from the level of origin of the loculus (or loculi) almost to the stigma. The alignment of the cells of the tract indicates an actual or potential surface where the lateral faces of the large semi-solid carpels have met and become confluent over the inner face of the intervening columnar sterile carpels which are reduced to little more than their midrib bundles. These bundles in the region of the ovary run close to the outer epidermis. Similar demarcation of the carpel boundaries in the ovary occurs in *Tulipa* (Liliaceæ) (see Vol. I, Part 2, pp. 63, 64) and in *Gossypium* (see under Malvaceæ, in Vol. I, Part 4, p. 110; also 27, Figs. 25-27). These three genera constitute a series in which *Pittosporum* occupies a middle position, for in *Tulipa* the sterile carpels with their midribs (which become split in half) contribute to each stigma lobe a small flanking portion representing half a carpel, so that each lobe consists of  $\frac{1}{2} \times \frac{1}{2}$  carpels, while in *Gossypium*, the sterile carpels have disappeared at so low a level that they can barely be said to have an existence.

At the flower base the sepal midribs, which form true lateral veins, and the stamen bundles turn out in succession from the central vascular cylinder on the one set of radii; the petal midrib bundles similarly turn outwards on the alternate set of radii. At the same time some of the residual elements of the cylinder turn inwards to the centre where they eventually become organised into the placental bundles of the fertile carpels. The remaining residual elements form a new ring of many small bundles of which single equidistant ones become the midrib bundles of three or two sterile carpels. Those lying in the intervening sectors form that portion of the systems of an equal number of alternating fertile carpels corresponding with the midribs of the sterile carpels, these portions becoming much reduced above the level of the disc-like tissue.

**Sollya** G 2, sterile + 2, fertile. Ovary bilocular below, becoming unilocular above as the fertile carpels no longer extend to the centre. Stigma concave, obscurely lobed. Fruit a berry.

The well-developed sterile carpel midrib bundles run upwards so close to the border of the loculi that it can hardly be supposed that fertile carpel tissue intervenes between these midribs and the loculi as in *Pittosporum* (see above), though were it in fact to do so, the intervening cell layers are too few in which to detect a definite radial tract indicating a line of junction such as occurs in *Pittosporum*.

**Cheiranthra.** Ovary and fruit as in *Sollya* (see above).

The simple character of the vascular system in this genus renders it particularly easy to trace the origin of the bundles of the different whorls.



## 44. HAMAMELIDACEÆ

Flowers ♂, polygamous or unisexual and monœcious, generally isomerous in the outer whorls but with reduction in the gynæceum; when most fully developed, six-whorled, but sometimes five-whorled through suppression of the corolla; more or less syngonous. Perianth whorls tetramerous or pentamerous. Antepetalous staminal whorl generally staminodal. Gynæceum dimerous, syncarpous below, becoming pseudo-apocarpous above. Ovary of 2 median, sterile and 2 lateral, fertile carpels, bilocular throughout or unilocular at the level at which the fertile members fail to reach the centre. Ovules sometimes several in each loculus (Bucklandioideæ), more often becoming solitary through the non-development of a second primordium and then pendulous from the top of the loculus (Hamamelidoideæ). Styles 2, centred over the sterile carpels, each of  $\frac{1}{2}$  +  $\frac{1}{2}$  carpels. For as the gynæceum becomes pseudo-apocarpous the fertile carpels undergo median radial splitting, hence each style is formed of a whole sterile carpel flanked on each side by half a fertile carpel. Stigmas 2, terminal or extending down the inner face of each style. Fruit capsuloid, generally splitting loculicidally in the upper pseudo-apocarpous region into four valve-like segments.

## ILLUSTRATIVE TYPES

## HAMAMELIDOIDEÆ

Ovules solitary in the loculi.

**Corylopsis.** Flower ♂. K 5, with commissural marginal veins C 5 A (generally) 5 + 5<sub>1-3</sub>, staminodal G 2, median, sterile + 2, lateral fertile.

The enlarged central vascular cylinder at the flower base consists of a ring of ten trunk cords on equidistant radii.

The sterile carpel midrib bundles are detached from the two cords standing in the median plane back and front, the one on a sepal, the other on a petal radius. The fertile carpel midrib bundles are similarly detached from two opposite cords lying nearest to the lateral plane on a sepal and a petal radius, respectively. The corresponding placental strands organised from elements detached from the original trunk cords at a lower level lie in the centre in line with the fertile carpel midribs. At a higher level a bundle is detached from each of the trunk cords on the sepal radii to become the bundle of an antesealous fertile stamen. When, as in most flowers, ten staminodes are present, they stand in pairs in front of each petal. Each trunk cord on a petal radius gives off a pair of lateral branches. The residual central portion of these cords becomes a petal midrib, the laterals enter the superposed pair of staminodes but soon cease. This inter-relation between the vascular systems of the corolla and a duplicated antepetalous staminal whorl is paralleled in some *Prunus spp.* (see under Rosaceæ later in the present Volume, Part 5, p. 177) where multiplication of the stamens representing the antepetalous staminal whorl occurs, and where also the stamens standing in front of each petal are served by lateral veins from the corresponding petal midrib. Again, in *Peganum Harmala* (Zygophyllaceæ) the antepetalous staminal whorl is duplicated as in *Corylopsis*, and here also the bundles serving the pair of stamens in front of each petal are given off on each side of the petal-midrib (see Vol. I, Part 3, pp. 87, 88 and Fig. 5; see also *Monsonia* and *Sarcocaulon* (Geraniaceæ and *Hypseocharis* (Oxalidaceæ) in Vol. I, Part 3, pp. 72 and 73, respectively)).

Styles becoming channelled and stigmatic along the inner face as the stylar canal opens to the surface through the median radial splitting of the fertile carpels. Each style receives a sterile carpel midrib bundle and one of the twin placental bundles of each of the two fertile carpels, but these latter bundles soon cease to be differentiated. As these bundles come to an end the persisting sterile carpel bundle gives rise to a branch system and the style apex assumes the broad, flattened, concave form often occurring in styles formed of a single valve carpel.

**Hamamelis** (Witch Hazel). Flower ♂. K 4, with commissural marginal veins C 4 A 4 + 4, staminodal, non-vascular G as in *Corylopsis* (see above).

The antesealous stamen bundles, as in *Corylopsis*, are carried out conjoined with the sepal midrib bundles. Those

for the antepetalous stamens arise conjoined with the petal midrib bundles.

**Parrotia persica.** Flowers ♀ or polygamous. K 5-7 C o A 5-7 antesepalous, antepetalous staminodes wanting, G as in *Corylopsis* (see above).

Flowers which become ♂ through loss of the fertile carpels (G 2 + o) have numerous stamens (up to 21) standing in a single ring. In these flowers staminal vascular bundles are detached, not only from the midribs of the sepals, but also from the primary pair of lateral veins. Only the midrib bundles of the sterile carpels are present in the gynæceum. The fertile carpels being suppressed there are no placenta, no placental bundles and no ovules.

**Fothergilla involucrata (Parrotiopsis Jacquemon-tiana)** K 5-7 C o A 5<sub>3</sub>-7<sub>3</sub> antesepalous G as in *Corylopsis* (see above).

The staminal vascular bundles, as in *Parrotia persica*, are detached from the sepal lateral veins as well as from the midrib bundles and stand in a single ring. But this multiplication of the antesepalous members of the andrœcium which in *Parrotia persica* occurs only in ♂ flowers obtains in *Fothergilla involucrata* in ♀ flowers.

## 45. PLATANACEÆ

Flowers unisexual, monœcious, the two sexes in separate spherical clusters, the ♂ clusters on lower, the ♀ on upper branches. Both ♂ and ♀ flowers generally with isomerous 3- or 4-, sometimes 6- or 8-merous whorls and often with rudiments of the non-functional sex. ♂ Flower. Sepals very small, scale-like with a hairy tuft. Petals also small and scale-like, sometimes fewer than the sepals by suppression. Stamens antesepalous with very short filaments. Anthers adnate, surmounted by the enlarged truncate end of the connective. Separate rudimentary carpels sometimes present in the centre. ♀ Flower hypogynous. Sepals and petals scale-like. Staminodes antesepalous. Gynæceum apocarpous. Ovaries antepetalous, monocarpellary, unilocular, passing gradually without definite boundary into a filamentous, hooked style which is grooved and stigmatic down the ventral surface where the stylar canal opens to the surface. Ovules solitary or very rarely two, pendulous from near the top of the loculus. Individual fruits 1-seeded, indehiscent.

In the ♂ flower only the stamens are vascular, the vascular system serving each flower consisting of a ring of as many separate bundles as there are stamens. When the flowers have withered and fallen the surface of the axis of the cluster is marked off by the intervening ground tissue, now become lignified, into areas corresponding with the individual flowers, each area being pitted with the scars of the broken vascular bundles corresponding in number with the fallen stamens. In the ♀ flower all the members receive a differentiated or undifferentiated vascular strand. As each ovary takes shape the corresponding carpel bundle turns outwards. Two placental strands are detached from it at once and are left behind on the same radius.

## ILLUSTRATIVE TYPES

**Platanus** (Plane). See the characters of the Family.

## 46. ROSACEÆ

Flowers generally ♂, sometimes polygamous or unisexual and diœcious, rarely monœcious, cyclic or hemicyclic; usually actinomorphic but the gynæceum often adherent at the base to one side of the flower wall, rarely zygomorphic; perigynous (5, pp. 206-224). [It must be understood that the term perigyny is used here in its widest sense, *i.e.* to cover every grade from that at one end of the scale in which the greater part of the gynæceum is enclosed in, and ultimately fused with, the concave summit of the axis as in Pomoideæ, through that in which the whole gynæceum lies free in such a 'cup' as in *Rosa*, to that in which the free gynæceum is borne on a flat or even convex receptacle, but in which the sepals and petals, being borne on the surrounding rim, stand at a higher level.] Since it is often difficult to determine whether any axial tissue enters into the formation of the common structure from which sepals, petals and stamens apparently spring, or whether it is composed entirely of the fused basal portions of these whorls, the convenient term flower wall is used here and elsewhere to denote this structure where it is of doubtful or complex nature.

The perigynous condition often presents much difficulty in the interpretation of the floral construction owing to 'condensation' (anastomoses and fusions) in the vascular scheme when elongation of the stem apex ceases early. This difficulty is intensified when the condition is accompanied by reduction in the number of carpels, or by degeneration of the vascular bundles, or by both features. It is well exemplified in such rosaceous genera as *Waldsteinia* and *Agrimonia* (7, pp. 576 and 611-613), for in such types the criteria of radial alignment cannot be applied. In this connection it is to be noted that an earlier interpretation of the gynæceum of *Waldsteinia* (see above citation) ought probably to be revised. Analogy with certain other reduced types in which the appearance seems opposed to a monocarpellary construction indicates that each

*Waldsteinia* ovary may correspond, as in these other types, not with a single carpel, but with  $\frac{1}{2} \times 1 \frac{1}{2}$  carpels. (See also later under *Agrimonia* among Illustrative Types, p. 176.)

Sepals generally with commissural marginal veins. Stamens often 20 ( $5 + 15$ , an arrangement particularly easily observed owing to the absence of a gynæceum, in male flowers of *Aruncus silvester* after they have been rendered transparent in chloral hydrate), but sometimes more numerous (40–60), less often 10 ( $5 + 5$ ), rarely 5 or fewer. Numbers higher than 10 result from multiplication of the members of the antepetalous whorl or less often of both whorls. The vascular bundles for both staminal whorls are always carried out from the central cylinder conjoined with the sepal and petal midrib bundles, respectively. It follows that the radial position of the carpels is unaffected by variations in the number of stamens present. A genus may include some species having only members of one staminal whorl and others having members of both whorls, but the carpels will naturally in the above circumstances occupy the same position in all the species. Gynæceum generally acyclic and apocarpous or cyclic and pseudo-apocarpous (see Vol. I, Introduction, p. 2), sometimes cyclic and syncarpous. Individual ovaries of the apocarpous gynæceum monocarpellary, those of the pseudo-apocarpous form consisting of  $\frac{1}{2} \times 1 \frac{1}{2}$  carpels. These three gynæceal forms are precisely comparable with those in Ranunculaceæ represented by *Anemone* and *Clematis*, by *Eranthis*, and by *Nigella*, respectively (see under that Family in Vol. I, Part 2, p. 36). Fruit various (achene, follicle, capsule, drupe), sometimes a pseudocarp.

Owing to the great diversity in the floral relations occurring within the Family further details of structure together with the descriptions of Illustrative Types are most conveniently given under each section.

(ia) SPIRÆOIDEÆ-SPIRÆÆ (7, pp. 600, 601, Figs. 147-156 and pp. 605-610, Figs. 180-182 and 185-188).

Flower cyclic throughout, generally ♂, six-whorled and pentamerous, but sometimes with an oligomerous gynæceum. Calyx, corolla and andrœcium united below for a longer or shorter distance into a funnel-shaped flower wall, becoming disjoined above. Sepals generally with commissural marginal veins. Stamens rarely 10 (5 + 5); through multiplication of the antepetalous members generally 20 (5 + 15), sometimes 30 or more. Numbers higher than 10 result when the antepetalous stamen members are represented not only by an unpaired stamen of which the vascular bundle is disjoined from the petal midrib but also by pairs of stamens the bundles of which are disjoined from the paired lateral veins of these midribs (see also under Hamamelidaceæ earlier in the present Volume, Part 5, p. 163). The unpaired and paired antepetalous filaments usually become free from the calyx-corolla-andrœcium wall at different levels, and the antesepalous filaments (which similarly spring from the flower wall) at yet another level. These differences in level give rise to the illusory appearance that the andrœcium is composed of more than the normal two whorls. Central parenchyma of the axis prolonged above the level of origin of the gynæceum (*Sorbaria*, *Sibiræa*, *Gillenia*) or ceasing below (*Spiræa*, *Stephanandra*). Carpels 5, 3, 2 or 1 in each whorl. If isomerous with the outer whorls the outer, sterile carpels (and loculi) are antesepalous when the central parenchyma of the axis is prolonged; antepetalous when it ceases below the gynæceum. Gynæcea with more than one carpel in each whorl rarely syncarpous, usually becoming pseudo-apocarpous through median radial splitting of the fertile members. Each partially separate ovary so formed consists of  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels and gives rise to a follicle which dehisces down the ventral

suture if the ventral surface is free through the cessation of the central parenchyma, down the dorsal mid-line if the axial tissue is prolonged and continuous with the ventral face. (For the definition of the term follicle see Vol. I, Part 2, p. 36.) In syncarpous types in which the axial parenchyma is prolonged into the ovary the fruit is of capsule form and similarly splits down the dorsal mid-line (so-called dorsal suture).

### ILLUSTRATIVE TYPES

**Sorbaria**, **Sibiræa**, **Gillenia** (all included formerly under *Spiræa*), **Spiræa**. These four genera, though closely related, vary in the shape of the floral axis (whether convex or concave at the summit); in the number of stamens arising from multiplication of the antepetalous members; in the character of the whole gynæceum (whether syncarpous or pseudo-apocarpous); in the radii of origin and in the orientation of the carpels (whether antesepalous or antepetalous and whether remaining aligned with the radii of origin or becoming inclined tangentially to the flower wall); and in the direction of development of the carpellary vascular system (whether centrifugal or centripetal).

**Sorbaria** (*e.g.* **S. Aitchisonii**, **S. assurgens**, **S. sorbifolia**) (7, pp. 608, 609, Figs. 180-182). Flower ♀ A 5 + 5<sub>7-11</sub>. Flower wall forming a deep funnel. Gynæceum syncarpous. Central parenchyma of the axis prolonged above the level of origin of the carpels and loculi. Carpels remaining aligned on the radii of origin. Fruit of capsule form dehiscent down the dorsal mid-line. Sterile carpal midrib bundles carried out from the central vascular ring conjoined with the sepal-stamen trunk cords, hence these carpels and the loculi are antesepalous.

**Sibiræa lævigata**. Flowers polygamous and dioecious. The central parenchyma of the axis is prolonged in the ♀



flower, as in *Sorbaria* (see above), above the level of origin of the carpels, but the gynæceum differs from that of the latter genus in being pseudo-apocarpous. Carpels remaining aligned on the radii of origin. The sterile carpel midrib bundles turn out from the central cylinder independently and therefore naturally, in the absence of an andrœcium, on the sepal radii. Hence, the partially separate ovaries and the loculi are antesepalous.

**Gillenia trifoliata.** Flower ♂. Flower wall as in *Sorbaria* (see above).  $A\ 5 + 5_{1-3}$ . Gynæceum pseudo-apocarpous. Owing to the cessation of the axial parenchyma, the fertile carpels become free on their ventral face before the outer surface of the ovaries is disjoined from the flower wall, so that the median splitting takes place from the centre outwards. The sterile carpel midrib bundles differ from those of *Sorbaria* in that they turn out from the central cylinder independently but, as in *Sorbaria*, they lie on the sepal radii (see above). Hence the ovaries and loculi are antesepalous in origin. This alignment with the sepals is not maintained, for being free from the base upwards on their ventral face, the ovaries gradually become turned sideways.

**\*Spiræa** (e.g. **\*S. salicifolia**, **S. chamædrifolia**, **S. Henryi**, **S. Thunbergii**) (7, pp. 605-607 and Figs. 147-150). Flower ♂. Floral axis concave through early cessation of the central parenchyma.  $A\ 5 + 5_{3-5}$ . Gynæceum pseudo-apocarpous. The five ovaries, free on their ventral face before being disjoined from the flower wall on their dorsal face, become turned sideways. The early cessation of elongation of the stem apex is accompanied by a process of 'condensation' in the development of the gynæceal vascular system. This is derived from elements detached from the inner face of the central cylinder on both sets of radii. Those elements lying on the petal radii are organised into the sterile carpel midribs. Those on each sepal radius represent the system of a fertile carpel. This disposition is the reverse of that in the three preceding genera in which the axis is convex, and at present is unexplained. Each fertile carpel system becomes divided in half, and as the ovaries take shape on the inner face of the flower wall each receives a sterile carpel midrib and half the vascular system of the neighbouring fertile member on each side. As in *Gillenia* (see above) the gynæceum is pseudo-apocarpous from the outset, and the ovaries, free on their ventral earlier than on their dorsal face, become turned sideways.

Exceptionally, only four ovaries may be formed in a flower otherwise pentamerous. When this condition occurs as near

an approach as possible to complete actinomorphic symmetry is achieved by the development of one of the ovaries (and therefore of a sterile carpel and loculus) in line with a sepal, the other three being, as usual, antepetalous (unpublished).

**Stephanandra** (7, pp. 607-609 and Figs. 151-156). Floral axis concave as in *Spiræa* (see above). The gynæceum is reduced to a single syncarpous ovary composed of two whole carpels, one sterile, one fertile, one on the radius of a sepal, the other on that of the opposite petal. Vascular elements which serve the four missing ovaries are present on the other radii, but they are undifferentiated and shortly cease. The solitary ovary becomes free on the ventral earlier than on the dorsal face and, as in similar circumstances in *Spiræa* (see above), becomes turned sideways.

#### (ib) SPIRÆOIDEÆ-QUILLAJEÆ (7†)

Flowers generally ♂, sometimes polygamous and diœcious. Central parenchyma of the axis prolonged above the level of origin of the syncarpous or pseudo-apocarpous gynæceum. Stamens generally > 10 through multiplication, rarely 10 (5 + 5) or 5. Carpels generally 5, sterile + 5, fertile or 3, sterile + 3, fertile. When isomerous with the outer whorls sterile carpels and loculi antesepalous. Fruit dehiscing down the ventral sutures when they are free through cessation of the axis parenchyma; in the mid-line of the sterile carpels when the central parenchyma is prolonged.

### ILLUSTRATIVE TYPES

**Exochorda** (7, p. 611 and Figs. 183-188). Flowers polygamous and diœcious. G (generally) 5 + 5, pseudo-apocarpous. The axial parenchyma is prolonged far up the gynæceum. Consequently the antesepalous ovaries retain their radial position and when ripe split along the mid-line of the sterile carpels.

#### (ii) POMOIDEÆ (5, pp. 206-224†, and 7, p. 610 and Figs. 178, 179)

Flower ♂, six-whorled and pentamerous throughout (K 5 C 5 A 5 + 5 G 5, sterile + 5, fertile) or sometimes with an oligomerous gynæceum. Floral axis in general concave forming a 'cup'. In the wall of the 'cup' a separate, superficial axial vascular system apart from that of the central cylinder. Axial parenchyma prolonged

from the bottom of the 'cup' as far as, or above, the level of origin of the carpels and loculi. Lining the axial 'cup' and fused with it the base of perianth and androecium, forming at this level a continuous wall of tissue in which run upwards ten trunk cords serving, respectively, the five sepals and antesepalous stamens, and the five petals and antepetalous stamens. Sepals and petals becoming free at the rim of the 'cup.' Sepals generally with commissural marginal veins. Stamens  $> 10$  ( $5 + 5$ ) through multiplication of the antepetalous members. Sterile carpels (and loculi) when 5 antesepalous, the midrib bundles being organised from the same vascular units as the sepal and antesepalous stamen bundles. These units may be resolved into the sepal-stamen and carpel components at the boundary of the central cylinder or not until they have turned outwards. When fewer than 5 some of the sterile carpel midribs are detached from the antesepalous vascular units, some from the antepetalous units, so that they are spaced as equally as the numerical relations permit. Styles generally terminal, centred over the sterile carpels; connate at first or free to the base (*Osteomeles*). Sometimes lateral (*Cotoneaster*). Fruit a pseudocarp, the gynæceum being enclosed in the tissue of the 'cup' which becomes fleshy.

### ILLUSTRATIVE TYPES

**Chænomeles Lagenaria** (*Cydonia japonica*) (5, Figs. 15-33). Gynæceum almost completely over-arched by the axis. Central parenchyma prolonged for a considerable distance into the ovary. Sterile carpel midribs carried out from the central cylinder conjoined with the sepal-stamen trunk cords, hence these carpels (and the loculi) are antesepalous. Each style with a terminal central and twin lateral stigmatic surfaces corresponding with its formation from  $\frac{1}{2}$  &  $\frac{1}{2}$  carpels.

**\*Pirus communis** (Pear) (5, Figs. 1-14). **\*P. Malus** (Apple), **\*P. Aucuparia** (Mountain Ash, Rowan tree). Central parenchyma prolonged less far into the ovary than in *Chænomeles* (see above). Sterile carpel midribs organised from the same vascular units as the sepal-stamen trunk cords but becoming dissociated from these cords nearer to the central cylinder than in *Chamæmeles* (see above). In the fruit of the apple and pear the carpels give rise to the cartilaginous core which is embedded in the abundant flesh of the axis.

**Amelanchier** (7, p. 610 and Figs. 178, 179). Sterile carpel midribs carried out clear of the central cylinder conjoined with the sepal-stamen trunk cords. The axial parenchyma ceases shortly above the level of origin of the loculi leaving the inner face of the fertile carpels free. The sterile carpels project into the loculus as incomplete partitions.

#### (iiiia) ROSEOIDEÆ-KERRIÆ (7†)

Receptacle flat or slightly concave. Stamens  $> 10$  ( $5 + 5$ ) through multiplication. Gynæceum pseudo-apocarpous. Ovaries generally 5 or 4. The sterile carpel midribs turn out from the central cylinder independently. Each ovary receives in addition to this midrib half the vascular system on the alternate radius on each side corresponding to half the system of a fertile carpel; hence each represents  $\frac{1}{2} \times \frac{1}{2}$  carpels. When isomerous with the outer whorls the ovaries are antesepalous or antepetalous according to the number of outer whorls present and the shape of the receptacle. They become free on their dorsal face while still concrescent on their ventral face, hence they retain their radial alignment. Individual fruits one-seeded, indehiscent, drupaceous.

#### ILLUSTRATIVE TYPES

**Kerria japonica** (7, pp. 604-605, and Figs. 197-199). Corolla present. Ovaries 5, antesepalous.

**Neviusia alabamensis** (7, p. 605 and Figs. 166-168). Corolla absent. Ovaries 5, antepetalous.

**Rhodotypus kerrioides** (7, pp. 603-604 and Figs. 143-146). Flower with epicalyx, tetramerous. A corolla is present. Nevertheless the isomerous ovaries are antepetalous. This break in the alternation of whorls having vascular bundles of independent origin is not uncommon in tetramerous types. It would appear that as the receptacle becomes four-sided it is the greater amount of available room on the diagonal as compared with the orthogonal radii rather than the normal rhythm of strict alternation which determines the position of the fifth (sterile carpel) whorl when the corresponding vascular bundles arise independently. (See also under Lythraceæ later in the present Volume, Part 8, p. 273.)

(iii*b*) ROSEOIDEÆ-POTENTILLEÆ (7, pp. 611-613†)

An epicalyx often present. Central parenchyma of the axis prolonged above the flower base in the form of a cone. Stamens almost always  $> 10$  ( $5 + 5$ ) through multiplication. Gynæceum acyclic and apocarpous. Ovaries generally numerous, sometimes few, monocarpellary. Individual fruit generally an achene, sometimes succulent.

### ILLUSTRATIVE TYPES

**\*Potentilla Tormentilla** (7, Figs. 189-191). Epicalyx present. Ovaries few. The vascular bundles for the several ovaries become defined below the level of exsertion of the carpels, one bundle passing into each ovary as the carpel midrib which gives rise to the placental strand on the same radius. Individual fruit an achene.

**\*Fragraria vesca** (Strawberry). Epicalyx present. Fruit a pseudocarp consisting of the succulent receptacle in which are embedded the numerous seed-like achenes.

**\*Rubus fruticosus** (Blackberry). No epicalyx. Receptacle dry, carpels (ovaries) becoming succulent, the whole fruit being thus a collection of small drupes.

(iii*c*) ROSEOIDEÆ-CERCOCARPEÆ (7, p. 611†)

Flower wall tubular. Corolla sometimes wanting. Stamens  $> 10$  ( $5 + 5$ ) through multiplication. Gynæceum syncarpous,

of a single central dimerous ovary (or of two such ovaries through bipartition of the axis above the level of origin of the perianth-stamen bundles). The residual vascular elements serving the gynæceum constitute a complete cylinder. Sterile carpel midrib and fertile carpel placental bundle become organised at opposite points of the cylinder.

## ILLUSTRATIVE TYPES

**Cercocarpus.** Corolla absent (7, Figs. 169-175).

**Purshia tridentata.** Corolla present (7, Figs. 176, 177).

## (iiid) ROSEOIDEÆ-ULMARIEÆ (25, pp. 848-852)

Receptacle flat or slightly concave. Flower ♂. A 20-40 through multiplication of both the antesealous and the antepetalous members, the filaments standing one above another on each radius. Gynæceum acyclic, apocarpous. Ovaries 5-15 monocarpellary. Each ovary with two placental strands derived from the midrib and two ovules.

## ILLUSTRATIVE TYPES

**\*Filipendula Ulmaria** (formerly included in *Spiræa*) (Meadowsweet). Ovaries 5-8, twisted. (25, Figs. 1-5.)

**\*Filipendula hexapetala** (formerly included in *Spiræa*) (Dropwort). Ovaries 6-12, not twisted (25, Figs. 6-11).

## (iiie) ROSEOIDEÆ-SANGUISORBEÆ (7, pp. 570-576† and 16, p. 110†)

Flower wall tubular or sack-shaped. Flowers generally ♂, sometimes unisexual, monœcious or diœcious. Epicalyx sometimes present. Perianth whorls frequently tetramerous, less often pentamerous. Corolla sometimes wanting. Stamens in ♂ pentamerous flowers rarely > 10 through multiplication, mostly 10 (5 + 5); in tetramerous types generally isomerous with the sepals and superposed upon them (4 + 0) or fewer. Gynæceum syncarpous, of a single dimerous ovary of one sterile and one fertile

carpel; or through division of the axis above the level of origin of the perianth-stamen bundles of 2-4 similar ovaries. Fruit generally enclosed in the flower wall.

### ILLUSTRATIVE TYPES

\****Alchemilla vulgaris*** (Lady's Mantle). Flower ♂, tetramerous. Epicalyx present. Corolla wanting. A 4 superposed on the sepals. Ovary single, of one sterile and one fertile carpel. Style 'gynobasic,' standing over the placenta. Stigma capitate, entire. (See 7, Figs. 19-24 and 16, p. 110, Fig. 18.)

\****Poterium Sanguisorba*** (Salad Burnet). Flowers unisexual, monœcious, tetramerous. No epicalyx. ♀ Flower. Ovaries 1 or 2, dimerous as in *Alchemilla* (see above; also 7, Figs. 15-18). Style(s) terminal. Stigma(s) brush-like.

\****Agrimonia Eupatoria*** (Agrimony). Flower ♂. Calyx and corolla pentamerous. A 10 (5 + 5)—20 or more through multiplication. Ovaries 2 or 3, probably arising through partition of the axis, each dimerous (see earlier statement, p. 166). Sterile carpel without a differentiated midrib bundle.

(iii f) **ROSOIDEÆ-ROSEÆ** (7, p. 614 and Figs. 193, 194)

Floral axis deeply concave as in Pomoidæ and with a superficial vascular system but without a central prolongation of the axial parenchyma (see above, p. 171). A  $\infty$  owing to multiplication. Gynæceum acyclic and apocarpous. Ovaries numerous, monocarpellary, springing from the base and sides of the axial 'cup.' Fruit a pseudocarp formed of the whole gynæceum enclosed within the fleshy receptacle.

### ILLUSTRATIVE TYPES

\****Rosa* spp., e.g. *R. moschata***. See the characters of the section.

## (iv) PRUNOIDEÆ (7, pp. 576-603†)

Flowers polygamous-dioecious or ♀. Flower wall cup-shaped. A 10 (5 + 5), or 20 or more through multiplication of the antepetalous members only or of the antesepalous members as well. Gynæceum either pseudo-apocarpous, the ovaries being then isomerous with the perianth whorls, springing from the inner face of the flower wall, antepetalous, and consisting of  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels as in *Spiræa* (see above, p. 170). Or syncarpous, of a single, central, dimerous ovary of one sterile and one fertile carpel.

## ILLUSTRATIVE TYPES

**Nuttallia cerasiformis** (7, pp. 601-603 and Figs. 140-142). Flowers polygamous-dioecious. Gynæceum pseudo-apocarpous. Ovaries 5, each of  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels.

\***Prunus** (Plum, Cherry, Apricot, Sloe or Blackthorn, Bird-Cherry, Cherry-Laurel), **Amygdalus** (Almond, Peach) (7, Figs. 26-139). Flower ♀. A frequently 20 through trebling of the antepetalous members (5 + 5<sub>3</sub>) as, e.g., in *P. cerasiferus* (Mirabel Plum), sometimes 35 through doubling of the antesepalous members and quintupling of the antepetalous members (5<sub>2</sub> + 5<sub>5</sub>) as commonly in *A. communis* (Almond). The two stamens representing each antesepalous member stand one over the other in the mid-line of the sepal. The staminal bundle derived from the sepal-stamen trunk cord gives off a strand to the lower of the two stamens, continues upwards in the same straight line and terminates in the upper one. The quintuplet representing each antepetalous member consists of one stamen in the mid-line of the petal, and two on each side standing one above the other. Only the middle unpaired stamen is supplied by the bundle derived directly from the petal-stamen trunk cord when it becomes resolved into petal midrib and staminal component. The bundles for the two stamens



on either side are detached successively from the primary pair of laterals developed from the petal midrib. Gynæceum reduced to a single central ovary of two carpels, one sterile, one fertile. Fruit a drupe.

As commonly in dimerous ovaries of one sterile valve and one fertile solid carpel with twin placental bundles the formation of the loculus results at once, or shortly, in a cleavage of the fertile carpel between these two bundles so that the loculus communicates by a channel with the exterior, the ovary wall becoming closed again immediately above this point by the reunion of the contact surfaces.

The derivation of the gynæceal vascular system from a complete residual cylinder and the differentiation of the sterile carpel midrib and of the fertile carpel twin placental bundles at opposite points is most easily appreciated in transverse sections of species in which the vascular ground-plan is on a comparatively small scale as, *e.g.* in *P. Padus* (Bird-cherry) and *\*P. avium* (Wild Cherry).

In some otherwise normal strains of Plum as *e.g.* the Victoria Plum (7, Figs. 78, 79) supernumerary miniature ovaries, generally open on the ventral face and without ovules, sometimes develop on the flower wall. These ovaries are formed of a single carpel. They occur sporadically through a carpeloid modification of individual stamens.

In certain double-flowered strains of *P. avium* (7, Figs. 105-113 and 119-130) with very many petals owing to petalody of the whole andræcium the residual vascular elements corresponding with those which serve the gynæceum of the single flower become organised into the systems of two separate sterile, foliar members, each with style and stigma. These strains thus afford indirect confirmation of the dimerous character of the normal gynæceum.

In a double-flowered strain of another species, *P. triloba* (7, Figs. 133-139), doubleness is due in part to buds which

develop in the angle between the flower wall and the end of the axis and which must be regarded as axillary structures.

(v) **CHRYSOBALANOIDEÆ** (7, p. 614†)

Flower wall tubular or cup-shaped. Flower zygomorphic or almost actinomorphic. A 10 (5 + 5) or numerous, rarely 5 or fewer. Ovary central and free from the flower wall or excentric and adherent to the wall. Style 'gynobasic.'

### ILLUSTRATIVE TYPES

**Parinarium** (7, Figs. 200–202). Flower wall tubular. Flower zygomorphic. A 10–20. Ovary excentric and adherent to the flower tube. G 3 sterile + 1 fertile (reduced from 3 + 3). Of the outer carpels only one enlarges to form a loculus; the other two take part with the fertile carpel in the formation of the thick style.

**Chrysobalanus** (7, Figs. 203, 204). Flower wall cup-shaped. Flower almost actinomorphic, the ovary shortly becoming free from the wall and remaining central. A ∞ G 3 + 1 as in *Parinarium* (see above), but the style is slender and formed from the unpaired sterile carpel.

(vi) **NEURADOIDEÆ**

Flower ♂, ± an epicalyx. K 5 C 5, contorted A 10 (5 + 5) G 10, sterile + 10, fertile. Ovary syncarpous. After the formation of the perianth and andræcium on a pentamerous scheme the ground-plan changes, for the ten sterile carpels stand in a single ring and constitute a single whorl alternating with the andræcium as a whole. Consequently they occupy a wholly new set of radii. The fertile carpels naturally follow on the same radii as the perianth and stamen members. The central axial parenchyma is prolonged, and the gynæceum remains conjoined with the flower wall almost up to the level of origin of the styles. As the central parenchyma comes to an end the ovaries begin to separate, through median radial splitting of the fertile carpels from their now free inner face outwards, hence the styles are distinct. Each is centred over the intervening sterile member and represents  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels, being channelled on the ventral face in line with the junction of the two half carpels. Stigma terminal, grooved along the line where the stylar canal opens up on the ventral face. Fruit opening at the summit over each loculus.

Sterile and fertile carpels lack a midrib bundle, only the twin placental bundles of each fertile carpel being developed.

These are prolonged into the styles, each style receiving two bundles representing half the vascular system of the neighbouring fertile carpel on each side.

In many flowers the carpels develop very unequally. The short styles and minute stigmas of those feebly developed then become hidden in the felt of hairs covering those reaching full development. Hence the illusory appearance that some carpels are missing.

### ILLUSTRATIVE TYPES

**Neurada.** Epicalyx present.

**Grielum.** No epicalyx.

## 47. CONNARACEÆ

Flower generally ♂, actinomorphic, hypogynous or slightly perigynous, pentamerous in the outer whorls, with an isomerous pseudo-apocarpous or an oligomerous syncarpous gynæceum (K 5 C 5 A 10 (5 + 5) G 5, sterile + 5, fertile or K 5 C 5 A 10 (5 + 5) G 1, sterile + 1, fertile). Sepals generally with commissural marginal veins. Stamens in completely isomerous types slightly obdiplostemonous. Filaments free or monadelphous at the base. Gynæceum when isomerous and pseudo-apocarpous of five antepetalous ovaries, each of  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels through median radial splitting of the fertile members; when dimerous of a single ovary.

Ovaries unilocular, with two ovules. Styles as many as the sterile carpels and centred over these carpels. Stigmas generally capitate, sometimes lappeted. Fruit single, capsuloid; or of 2-4 similar partial fruits splitting along the ventral line, or exceptionally, in the dorsal mid-line.

In types with a pseudo-apocarpous gynæceum composed of four or five ovaries (*e.g.* *Rourea*, *Agelæa*, *Cnestis*) median radial splitting of the fertile carpels, which generally takes place from without inwards, results in the formation of ovaries consisting of a whole sterile carpel flanked on each side by half a fertile carpel. If the central parenchyma of the axis is prolonged for a slight distance above this level the several ovaries may remain continuous with this tissue and may be held in position by it after becoming free from each other. If the axis parenchyma comes to an end below this level the several ovaries may become free on their ventral face while still being held in position by the flower wall from which they are not yet detached on their dorsal face.

When through reduction and 'condensation' of the residual vascular strands only a single ovary is present (as *e.g.* in species of *Connarus*), it is formed of two whole carpels, one sterile, one fertile. This extreme degree of reduction, which in the present Family is infrequent,

occurs with few exceptions throughout the nearly related and large Family of Leguminosæ (see later in the present Volume, Part 5, p. 184), and in a few genera among Rosaceæ (see under that Family earlier in the present Volume, Part 5, pp. 175, 178).

As a result (presumably) of the formation of the loculus (which does not make its appearance until the ovary, whether composed of  $\frac{1}{2}$   $1\frac{1}{2}$  or of 2 whole carpels, is completely free) the ovary wall becomes cleft in the ventral mid-line so that the loculus communicates with the exterior by a channel passing between the twin placental bundles, as in some Prunoideæ among Rosaceæ (see under this Family, *loc. cit.*, p. 178) and almost invariably in Leguminosæ (*loc. cit.*, p. 184), the ovary wall becoming sealed again immediately above this level through reunion of the cell layers bordering the channel.

### ILLUSTRATIVE TYPES

**Rourea fulgens, Agelæa vestita.** Flower hypogynous, generally pentamerous throughout (K 5 C 5 A 5 + 5 G 5, sterile, antepetalous + 5, fertile antesepalous). Andrœcium obdiplostemonous. Staminal filaments united only at the base. Gynæceum pseudo-apocarpous, median radial splitting of the fertile carpels taking place from without inwards as the gynæceum becomes free from the staminal ring, thus giving rise to separate ovaries consisting of  $\frac{1}{2}$   $1\frac{1}{2}$  carpels. As the loculus makes its appearance each ovary becomes cleft in the ventral mid-line, *i.e.* between the two placental bundles belonging, respectively, to the two fertile half carpels.

The antepetalous stamen bundles are organised from the same delimited group of vascular elements as the petal midrib bundles, hence the antepetalous position of the sterile carpels (and therefore of the loculi) (see Vol. I, Introduction, p. 8). But as these stamen bundles do not extend far from the central cylinder the obdiplostemonous relation is not strongly marked.

**Cnestis ramiflora.** Flower slightly perigynous, generally pentamerous throughout (K 5 C 5 A 5 + 5 G 5,

sterile + 5, fertile), scarcely obdiplostemonous. Gynæceum pseudo-apocarpous. Ovaries five, each of  $\frac{1}{2} \times 1 \frac{1}{2}$  carpels and cleft in the ventral mid-line as in the preceding types (see above).

The vascular scheme of the flower differs from that of the preceding types in that the bundles for the several whorls arise successively by the repeated break-up of the vascular units composing the enlarged central cylinder, the commissural lateral veins of the sepals, petal midrib, antepetalous stamen and sterile carpal bundles being detached in succession from those lying on the petal radii as each remnant turns inwards. As the antepetalous stamen bundles become detached at points scarcely further from the centre than those at which the antesepalous stamen bundles take up their position on the alternate set of radii the obdiplostemony is of the slightest. The residual vascular elements after a process of re-organisation give rise to the twin placental strands of a corresponding number of fertile carpels lying on the sepal radii.

**Connarus semidecandrus.** Flower slightly perigynous. Perianth and androecium pentamerous (K 5 C 5 A 5 + 5). The antepetalous stamen bundles carried out from the central cylinder conjoined with the petal midrib bundles. These stamens are generally sterile and very minute (hence the specific name). Gynæceum syncarpous. Ovary single, of two carpels, one sterile, one fertile; cleft as in *Rourea*, *Agelæa* and *Cnestis* in the ventral mid-line, the cleavage taking place in *Connarus* between the twin placental bundles of the single fertile carpal. The residual vascular elements for the gynæceum form a more or less complete cylinder as in most Cæsalpinoideæ and Papilionatæ (see later in the present Volume under Illustrative Types in these sections of Leguminosæ, Part 5, pp. 187 and 189), those elements occupying opposite points in the median plane become organised into the sterile carpal midrib and into the twin placental bundles of the fertile carpal, respectively; those on the intermediate radii either come to an end or merge with the bundles of the two median carpels.

## 48. LEGUMINOSÆ

Flower ♀, rarely through abortion unisexual, zygomorphic or actinomorphic, slightly perigynous, usually pentamerous, sometimes tetramerous, in the outer whorls, sometimes with numerous stamens. Gynæceum, except in three genera among Mimosoideæ (*Affonsea*, *Archidendron*, *Hansemannia*) and in two among Papilionatæ (*Arachis* and *Scorpiurus*) dimerous, of one sterile and one fertile carpel (3, pp. 142-146† and 11, pp. 225-258†). The vascular bundles of the andrœcium sometimes carried out from the central cylinder conjoined with the perianth bundles, sometimes arising independently. Ovary unilocular, very rarely bilocular at the base; generally cleft for a longer or shorter distance in the ventral mid-line about the level of formation of the loculus, as described in those genera among Rosaceæ and Connaræcæ having a syncarpous gynæceum consisting of a single dimerous ovary of one sterile and one fertile carpel or a pseudo-apocarpous gynæceum with  $>$  one ovary of  $\frac{1}{2}$   $\times$   $\frac{1}{2}$  carpels (see under these Families in the present Volume, Part 5, pp. 178 and 182, respectively). It is this feature, characteristic under certain conditions of ovaries of 1,  $\frac{1}{2}$   $\times$   $\frac{1}{2}$ , and 2 carpels which has, apparently, given rise to the mistaken conception that the legume arises laterally on the axis, the edges of this cleft having been taken to be the margins of a solitary, open carpel of which the opposite (anterior) vascular bundle is the midrib. But though this bundle is beyond doubt the midrib of a carpel, anterior and sterile, the above-mentioned 'edges,' except in *Arachis* and *Scorpiurus* (for these exceptional genera see below under Illustrative Types), constitute the central region of another carpel, posterior and fertile which, in the absence of a third median (midrib) bundle is split in the middle line between the twin placental bundles (see account

of the different types of carpels in Vol. I, Introduction, p. 10). The dorsal midrib and the ventral placental bundles are differentiated at opposite points of the residual vascular cylinder. The cylinder is prolonged in a straight line into the legume, which thus constitutes a terminal structure. Style single, centred over the sterile carpel. Fruit generally dehiscent down the mid-line of both carpels (*e.g.* *Pea*), hence, as a rule, the two valves of the fruit do not correspond with the two carpels; exceptionally, splitting at, or near, the lines of junction of the two carpels (*Medicago*) or tearing irregularly in this region (*Hæmatoxylon*), or indehiscent (*Arachis*, *Scorpiurus*). For the exceptional case of *Carmichaelia* see below.

### ILLUSTRATIVE TYPES

#### (i) MIMOSOIDEÆ (II, pp. 225–229†)

Flower actinomorphic.  $K\ 5$  (or  $4$ )  $C\ 5$  (or  $4$ )  $A\ 5$  (or  $4$ ), or  $5 + 5$  (or  $4 + 4$ ), or  $\infty$   $G\ 2$  ( $1 + 1$ ), very rarely  $2 + 2$ , or  $3 + 3$ , or  $5 + 5$ . Petals valvate. Stamen bundles turning out from the central cylinder independently.

***Albizzia lophantha*** (II, Figs. 4–8).  $A\ \infty$   $G\ 2$  ( $1 + 1$ ).

The residual vascular elements which furnish the bundles for the gynæceum form a ring of six bundles which become grouped into two triplets, one dorsal, one ventral. In the dorsal triplet the centre bundle is the strongest. It becomes the midrib bundle of the dorsal, sterile carpel. The two weaker ones serve as a pair of primary laterals. In the ventral triplet the median (midrib) bundle is the weakest and shortly disappears. The other two become the twin placental bundles of the ventral fertile carpel. In this way the residual vascular tissue for the gynæceum is transversely halved, the two equivalent halves serving two opposite carpels. The loculus makes its appearance immediately above the level at which the weak ventral bundle comes to an end. As these conditions obtain the wall of the ovary becomes furrowed in the ventral mid-line and then completely cleft from the surface to the loculus. At a slightly higher level the cleft is sealed as the edges come together and reunite.

***Leucaena glauca***.  $A\ 10$  ( $5 + 5$ )  $G\ 2$  ( $1 + 1$ ). In other respects similar to *Albizzia* (see above).



**Acacia spp.** (e.g. *A. suaveoleus* (II, Figs. 1-3), *A. longifolia*).  $A \infty G 2 (1 + 1)$ .

Six residual vascular strands arranged in two triplets serve the gynæceum as in *Albizzia* and *Leucæna* (see above), but in *Acacia* the centre bundle of the dorsal triplet is scarcely as strongly developed as the other two. As a result the ovary becomes furrowed (though not completely cleft) on the dorsal as well as on the ventral face.

**Mimosa pudica** (Sensitive Plant).  $A 4 G 2 (1 + 1)$ .

The residual vascular strands serving the gynæceum are reduced to five, the central strand of the ventral triplet having disappeared altogether. Reduction has thus been carried a stage further than in *Albizzia* (see above).

**Affonsea bullata**.  $A \infty$ . Gynæceum pseudo-apocarpous. Ovaries and styles 2, 3 or more.

The residual vascular system for the gynæceum consists of a well-developed central cylinder. This cylinder becomes broken up into two, three or more arcs. This premature segmentation is followed by the curving of each arc into a horseshoe-shaped unit (as seen in transverse section) with the ends directed towards the axis. The central portion of each 'horseshoe' gives rise to the midrib bundle of a sterile carpel; the elements on each side of the open end furnish one of the two placental bundles of the neighbouring fertile carpel on each side, these carpels standing on the alternate radii. In this way the vascular system of the fertile carpels becomes halved prematurely in accord with the early onset of the pseudo-apocarpous condition through median splitting from without inwards of the fertile members, which thus gives rise to ovaries of  $\frac{1}{2} \text{ } 1 \frac{1}{2}$  carpels. A somewhat similar early halving of vascular system and carpel is characteristic of some Ranunculaceæ having ovaries of  $\frac{1}{2} \text{ } 1 \frac{1}{2}$  carpels as e.g. *Eranthis*. Usually two or three ovaries are formed, representing a reduction from the full ground-plan of  $G 5 + 5$  to  $G 2 + 2$  or  $3 + 3$ .

**Hansemannia glabra**.  $A \infty$ . Gynæceum pseudo-apocarpous as in *Affonsea* (see above), but usually exhibiting the full ground-plan ( $G 5 + 5$ ) with formation of 5 ovaries each of  $\frac{1}{2} \text{ } 1 \frac{1}{2}$  carpels.

## (ii) CÆSALPINOIDEÆ (II, pp. 229-244†)

Flower zygomorphic or rarely almost actinomorphic.  $K 5 C 5 A 10 (5 + 5)$ , or by abortion fewer, very rarely numerous,  $G 2 (1 + 1)$ , one sterile one fertile. Petals

imbricate, the posterior member generally overlapped by the postero-lateral pair, these two being in turn overlapped by the antero-lateral pair.

**Cassia spp.** (e.g. *C. corymbosa*, 11, Figs. 22-29). Ovary with stipe.

Vascular system of the stipe forming a complete cylinder in which only two triplets of strands, situated opposite to one another in the median plane, develop xylem. The middle strand of the front triplet is stronger, that of the back triplet weaker, than the accompanying laterals. The strong central bundle becomes the midrib of the sterile carpel and is accompanied by the two laterals. The opposite weak middle bundle disappears. The two accompanying laterals become the twin placental bundles of the fertile carpel. The undifferentiated strands intervening between the triplets and completing the cylinder, i.e. the strands corresponding with the lost antero- and postero-lateral carpels of two pentamerous whorls, shortly cease to be traceable. After the weak median strand of the fertile carpel has come to an end the ovary wall becomes furrowed in the corresponding mid-line at the level of origin of the loculus.

**C. lævigata** (11, Figs. 12-21). Similar to *C. corymbosa* (see above), but without a central xylem-forming strand between the pair which become the placental strands.

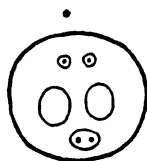
**Saraca indica** (11, Figs. 30-38, and 19*b*, p. 213). An exceptional type with a single coloured perianth, tubular below, divided above into four free segments although the vascular ground-plan of the perianth is of the normal type consisting of ten vascular bundles on the same radii as the ten stamens. Segmentation of the perianth occurs in such a way that each of two opposite segments receives three of these bundles and each of the other opposite segments two bundles. In this way each segment receives either one or two bundles proper to a petal radius, hence each is coloured.

**Hæmatoxylon campechianum.** A type with an exceptional fruit which when ripe becomes torn irregularly down the two sides, i.e. between the vascular systems of the two carpels. Consequently the two fruit valves, unlike those of the ordinary legume, correspond approximately with the two carpels.

- (iii) PAPILIONATÆ (3, pp. 142-146†, 11, pp. 244-258†, 18, pp. 184, 185†)

Flower zygomorphic.  $K\ 5\ C\ 5\ A\ 10\ (5 + 5)$ , monadelphous or diadelphous (9 and 1),  $G\ 2\ (1 + 1)$ , only in two genera (*Arachis* and *Scorpiurus*)  $> 2$ . Petals imbricate, the posterior member (standard) overlapping the posterolateral pair (wings) which in turn overlap the anterolateral pair (forming the keel).

Sepals generally with commissural marginal veins (see 18, p. 185, Fig. 9).



*Astragalus monspessulanus*. Base of the ovary in transverse section. (From 3, p. 145, Fig. 48.)

FIGURE 8.

\***Astragalus** (3, Figs. 48, 49 and 11, Figs. 69-74).  $G\ 2$ , one sterile, one fertile. A 'key' genus affording examples of forms (e.g. **A. monspessulanus**, **A. Tragacantha**) in which the main vascular systems of the two carpels are similar, each consisting of twin bundles. At the base of the ovary the two constituting the system of the sterile carpel are continuous, forming a single vascular unit, but its double nature is shown by the presence of two separate xylem strands (see Fig. 8); the two representing the system of the fertile carpel, as usual, are distinct. In many species the sterile carpel projects inwards in the mid-line so far as to render the ovary nearly or quite bilocular at the base. Fruit splitting down the mid-line dorsally and ventrally, i.e. in the mid-line of each carpel. Hence each fruit valve does not correspond with one whole carpel, but with half of each of the two carpels ( $\frac{1}{2} \frac{1}{2}$ ).

**\*Lathyrus spp.** (Pea) (11, Fig. 58). G 2, one sterile, one fertile.

Gynæceum with the type of vascular system characteristic of the bulk of genera in the Family, consisting of a well-marked midrib with a pair of primary laterals of a sterile carpel and the twin placental bundles of a fertile carpel, organised from opposite points of a complete residual cylinder. Fruit splitting down the mid-line dorsally and ventrally as in *Astragalus* (see above).

**\*Medicago** (Medick) (3, Figs. 41, 42, and 11, Fig. 67). G 2, one sterile, one fertile.

The residual vascular elements for the gynæceum are reduced from the outset to the midrib bundle of the sterile carpel and two strands which become the twin placental bundles of the fertile carpel. The spirally coiled fruit splits, along each side of the dorsal (sterile carpel) midrib through snapping of the short weak lateral veins of this midrib. Hence the two separate portions of the ripe fruit correspond very nearly to the two carpels, the broader segment consisting of the posterior semi-solid fertile carpel situated on the convex curve of the spiral, the narrower segment of the anterior solid sterile carpel on the concave curve.

**Carmichælia.** G 2, one sterile, one fertile.

The fruit shows an exceptional mode of dehiscence, splitting along each side of both the dorsal midrib and of the pair of placental bundles (which become enclosed in a common sheath of sclerenchymatous elements) through snapping of the few lateral veins. The two sides of the fruit fall away leaving behind a vertical oval frame formed of the main bundles of the two carpels. This frame simulates in appearance the replum of those Cruciferae in which it does not form a complete septum and the corresponding frame in the unilocular ovaries of those Papaveraceae and Capparidaceae in which  $G = 2 + 2$ . But whereas each of the two fruit valves in the two above-mentioned Families represents one whole carpel, each of those of *Carmichælia* is composed of portions of two carpels.

**Phaseolus vulgaris** (French Bean), **Baptisia alba** (11, Figs. 84-87). These species not infrequently produce exceptional flowers with two pods. This condition follows bifurcation of the axis above the level of origin of the perianth and stamen whorls and below that of the carpels. It is accompanied by constriction followed by complete halving of the

residual vascular cylinder at this level and the formation of two new cylinders. This duplication, which in these species is an exceptional feature, occurs in the normal course of development in some rosaceous forms, *e.g.* *Spenceria ramalana* where, however, reconstruction takes the place of simple constriction of the vascular cylinder.

***Arachis hypogæa*** (Pea Nut, Monkey Nut) (3, Figs. 43-45, and 11, Figs. 75-79), ***Scorpiurus* spp.** (3, Figs. 46, 47, and 11, Figs. 80-83). G 10 arranged in a single ring. In these two genera alone in the Family do the elements of the residual vascular cylinder serving the gynæceum become organised *on the radii on which they originally stand* into separate bundles corresponding in position with the ten construction radii and hence representing the bundles of the full number of carpels ( $5 + 5$ ). The ovary, therefore, may be compared in its construction to the tube of the monadelphous andrœcium. The two genera further agree in the following features. The weak bundle in the ventral mid-line immediately comes to an end and with it the corresponding carpel. Both the bundles (carpels) bordering this line are actually or potentially fertile, the remaining seven are sterile. In *Arachis* these seven carpels together with the fertile pair are all of similar form and solid, consequently the short 1-3 seeded fruit remains straight. In *Scorpiurus* the construction is similar except that the anterior carpel is of typical valve form and somewhat shorter than the rest, with the result that the long several-seeded fruit becomes spirally coiled with the valve carpel on the concave face. In both genera the ovary becomes cleft in the ventral mid-line as in other members of the Family and becomes sealed again above. The fruits are indehiscent, the plan of construction rendering resistance to rupture about equal on the different radii.

In the moulding in these two genera of the unreduced number of carpels into the same form of gynæceum as that in which reduction of the original carpel number has been carried to the limit ( $G = 2$ ), *Arachis* and *Scorpiurus* stand

in much the same relation to the bulk of leguminous genera as *Eschscholzia* to *Chelidonium* and similar types among Papaveraceæ (see under Illustrative Types in Papaveroideæ, Vol. I, Part 2, p. 49). In *Eschscholzia* each of the two sterile valves consists of a soldered block of nine carpels moulded into a single structure of valve form. In *Chelidonium*, in which reduction has reached the limit (here G 4), each of the two sterile valves of the fruit is formed of a single carpel.

The occurrence within the Leguminosæ of genera with an unreduced gynæceum side by side with others in which reduction has reached a maximum ( $G = 2$ ) is paralleled in the nearly related Family Connaraceæ (see earlier in the present Volume, p. 181). But whereas in Connaraceæ the formation of the full number of carpels is the general rule in Papilionatæ it is not only rare but the way in which retention of the full number has been achieved is different. For in *Arachis* and *Scorpiurus* the whole number of carpels come to stand in a single ring and only two are actually (or potentially) fertile, while in Connaraceæ the ten (or eight) carpels are arranged in the more usual way in two whorls, all those of the inner whole being fertile.



## Part 6

### Dicotyledons

Family	49.	Simarubaceæ
„	50.	Burseraceæ
„	51.	Malpighiaceæ
„	52.	Tremandraceæ
„	53.	Polygalaceæ
„	54.	Euphorbiaceæ
„	55.	Callitrichaceæ
„	56.	Buxaceæ
„	57.	Empetraceæ
„	58.	Coriariaceæ
„	59.	Anacardiaceæ
„	60.	Aquifoliaceæ
„	61.	Celastraceæ
„	62.	Aceraceæ
„	63.	Hippocastanaceæ
„	64.	Sapindaceæ
„	65.	Rhamnaceæ
„	66.	Vitaceæ





## 49. SIMARUBACEÆ

Flowers ♂ or unisexual by abortion, actinomorphic, hypogynous. Calyx, corolla and andrœcium generally isomerous and 5- or 4-merous (sometimes 3-, 6- or 7-merous). Stamens in two whorls or one-whorled through suppression sometimes of the antesealous, sometimes of the antepetalous whorl; when two-whorled usually obdiplostemonous. Between andrœcium and gynœceum usually a disc. Carpels 2-7, sterile + 2-7, fertile. Ovary syncarpous or through median radial splitting of the fertile carpels pseudo-apocarpous; sometimes through the very early stage at which this splitting takes place, simulating true apocarpy as in some Rutaceæ (see under that Family in Vol. I, Part 3, pp. 83-85). Styles generally united but with separate stigmas; in other types, sometimes wholly free, sometimes united only by the stigmas, sometimes united throughout; terminal or springing from the ventral face of the nearly separate ovaries. Ovules generally solitary, rarely 2 in each loculus. Fruit in pseudo-apocarpous types of several dry or drupaceous partial fruits; in syncarpous types a drupe with 2-5 one-seeded loculi.

### ILLUSTRATIVE TYPES

**Ailanthus glandulosa** (Tree of Heaven). Tree with abundant secretory canals. Flowers polygamous (♂, ♂, ♀), generally isomerous throughout ( $K\ n\ C\ n\ A\ n + n$ , obdiplostemonous  $G\ n$ , antepetalous, sterile +  $n$ , antesealous, fertile). Ovary becoming pseudo-apocarpous so early that it appears to be truly apocarpous. Ovules solitary in the loculi. Styles springing from the ventral face of the (at this level) separate ovaries, becoming conjoined above. Stigmas as many as the loculi and centred

over them. Partial fruits dry, winged, one-seeded, opening down the ventral face.

The vascular bundles for the antesealous stamens turn out from the central cylinder independently, those for the antepetalous stamens are carried out conjoined at first with the petal midrib bundles and become detached later. They thus come to lie farther from the centre than the antesealous bundles. The obdiplostemonous condition is emphasised further by the convex outline on these radii of the disc outside which the stamens arise. The sterile carpels are without midribs, these bundles having been lost, so that after the organisation of the sepal, petal, stamen and disc bundles, no vascular elements remain on the petal radii. Of those elements left on each alternate (sepal) radius, half serve one placenta and one half of the wall of the adjacent ovary on the one side, the other half serve the corresponding structures of the adjacent ovary on the other side. At the top of each ovary these two separate systems become 'condensed' into two bundles which enter the more or less 'gynobasic' style. Hence each ovary and each style corresponds with  $\frac{1}{2}$   $\times$   $\frac{1}{2}$  carpels if the non-vascular sterile carpel may be presumed to be prolonged between the two fertile half carpels.

**Quassia amara.** Flower ♂, pentamerous throughout. K 5 C 5 A 5 + 5, exerted below the disc and standing in one ring G 5, antepetalous, sterile + 5, antesealous, fertile. Gynæceum borne on a gynophore formed by elongation of the region of the disc, becoming pseudo-apocarpous at so early a stage as to simulate true apocarpy. Each of the five separate ovaries thus produced by premature halving of the fertile carpels consists of a sterile carpel flanked on each side by half the neighbouring fertile carpel ( $\frac{1}{2}$   $\times$   $\frac{1}{2}$ ). Ovules solitary in the loculi. Styles connate throughout, the single filament being traversed to the top by five separate tracts of conducting tissue. Stigma single, slightly five-lobed, the lobes standing in line with the sterile carpels. Fruit of five one-seeded, indehiscent cocci.

Sepals with true lateral veins. The vascular bundles for the two staminal whorls arise at about the same level. Owing to the development of a gynophore and its cylindrical form

the andrœcium is not appreciably obdiplostemonous. The residual vascular tissue serving the gynœceum consists of five units already situated on the petal radii below the level of the gynophore. These develop directly into the carpel bundles. Hence the interposition of the gynophore does not here affect the radial disposition of the carpels. (For the usual relation of a gynophore to the radial arrangement of the carpels see Vol. I, Introduction, p. 8.) The middle portion of each of these units turns outwards to become a sterile carpel midrib which is therefore antepetalous. The adjacent lateral portions of two neighbouring units furnish the twin placental bundles of an intervening antesepalous carpel. In consequence of the early onset of the pseudo-apocarpous condition these bundles do not, as ordinarily, converge to the sepal radius but remain apart.

## 50. BURSERACEÆ

Flower ♂ or through abortion unisexual, actinomorphic, hypogynous. Calyx, corolla and andrœcium isomerous, generally 3-5-merous. The andrœcium almost always in two whorls and obdiplostemonous. A ring-shaped disc often present between the andrœcium and gynœceum. Gynœceum syncarpous. Carpels 2-5, sterile + 2-5, fertile. Ovary with as many loculi as fertile carpels through union of these carpels in the centre. Sterile carpels and loculi in forms isomerous throughout antepetalous. Ovules generally 2, rarely 1, in each loculus. Style single with a terminal 2-5-lobed stigma, the lobes centred over the sterile carpels. Fruit drupaceous, either indehiscent or the exocarp splitting into 2-5 valves, with a 2-5-celled 'stone' or with 2-5 one-seeded 'stones.'

## ILLUSTRATIVE TYPES

**Canarium spp.** (*e.g.* **C. nitidum**). K 3 C 3 A 3 + 3, obdiplostemonous G 3, sterile, antepetalous + 3, fertile, antesepalous. Style thick. Stigma 3-lobed, each lobe of  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels through median radial splitting of the fertile carpels at the stigma level.

The vascular bundles for the antepetalous stamens do not originate independently, but are detached from trunk cords which also furnish the petal midrib bundles, hence the suppression of the antepetalous stamen whorl in some species does not affect the radial position of the succeeding (carpel) whorl; hence also the antepetalous position of the loculi in forms isomerous throughout. The vascular system of the fertile as well as that of the sterile carpels passes up the single thick style to the stigma level. Each stigma lobe receives the whole system of one sterile carpel and half the system of the neighbouring fertile carpel on each side. Fruit a 3-celled drupe.

## 51. MALPIGHIACEÆ

Flower almost always ♂ and hypogynous, zygomorphic with oblique symmetry, the plane of symmetry of the gynæceum being neither median nor lateral, generally with a pentamerous perianth and andrœcium and an oligomerous gynæceum. K 5 C 5 A 5 + 5, G 3, sterile + 3, fertile, seldom 2 + 2 or 4 + 4, still more rarely 5 + 5. Ovary syncarpous with as many loculi as sterile carpels through union of the fertile carpels in the centre, rarely pseudo-apocarpous, through early median radial splitting of these carpels. Ovules solitary in the loculi, pendulous. Styles 3 or 2 or 1, being sometimes as many as the loculi, sometimes fewer by suppression, but always standing over the loculi; sometimes springing from the centre between the lobes of the ovary, sometimes terminal arising by tapering upwards of the ovary without a sharp line of demarcation; each of  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels. Stigmas generally terminal. Fruit generally separating into as many segments as there are loculi through median radial splitting of the fertile carpels, the individual segments later opening in the dorsal mid-line through median radial splitting of the sterile carpels, each segment representing  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels; sometimes nut-like or drupaceous and indehiscent.

Calyx quincuncial, the plane of symmetry passing through sepal 3 (see p. 149, Fig. 7). Sepals with commissural marginal veins; sometimes with large external vascular glands. Midrib bundles of the sterile carpels feebly developed or wanting. The ovules being solitary in the loculi only half the placentæ are actually fertile. Since the ovules are not developed regularly on alternate placentæ, it follows that some fertile carpels may bear an ovule on each placenta, or only on one, while others may not develop an ovule on either. This irregular arrangement may possibly be the cause, at least in part, of the unequal development of the vascular bundles in the placentæ of different fertile carpels or of those in the two placentæ of an individual carpel, both conditions being of

common occurrence. When as many styles as loculi are formed, each receives a weak sterile carpel midrib (if these bundles are developed), together with half the vascular system of the fertile carpel on each side. If, as happens frequently in some genera, the vascular system of half the fertile carpel on each side of a sterile carpel comes to an end as the loculus closes, the corresponding style is not developed and the number of styles in such flowers is less than the number of loculi.

### ILLUSTRATIVE TYPES

***Tristellateia australis*.** Sepals without glands. Androecium slightly obdiplostemonous, actinomorphic. G 3 or 4, sterile + 3 or 4, fertile. Styles filamentous, channelled on the ventral face, springing from between the ovary lobes, 3, 2 or 1, but one alone fully developed, the other(s) present being shorter or quite rudimentary. Stigmas capitate. Fruit separating into segments.

The vascular bundles for both stamen whorls arise independently from the central cylinder. Sterile carpel midribs present, but feebly developed. Placental bundles unequally developed, only two representing half the fertile carpel on each side of one of the sterile carpel midribs usually reaching full development, hence only the corresponding style, which thus receives three vascular bundles, is fully developed. According as the two placental bundles bordering the other sterile carpels come to an end as the loculi close, or as one of these bundles is prolonged for some distance, the corresponding styles abort or, receiving one placental bundle in addition to the sterile carpel midrib, remain shorter than the style receiving three vascular bundles.

***Stigmaphyllon (Stigmatophyllum) littorale*.** Sepals with paired glands, generally 8, none being developed on sepal 3 which lies in the plane of symmetry. Androecium obdiplostemonous, zygomorphic through unequal development of individual members belonging to the same whorl, those in line with the gland-bearing sepals being sterile. G 3, sterile + 3, fertile. Styles as many as the loculi, springing from between the ovary lobes, generally equally developed. Stigmas large, terminal, concavo-convex,

bent downwards with the convex surface uppermost, with a projecting tuft of papillæ at the level at which the vascular bundles of the two fertile half carpels diverge in the style and come to an end, and the stylar canal opens to the surface on one side. Fruit splitting into segments.

The vascular system of the sepal glands is furnished by the commissural marginal veins. Stamens obdiplostemonous, the vascular bundles for the antepetalous whorl being conjoined at first with the petal midrib bundles, while those for the antesepalous whorl arise later direct from the central cylinder and extend less far from the centre. Sterile carpels without a differentiated midrib bundle, its place being taken by a longitudinal column of cells differing in appearance from the surrounding tissue. The twin placental bundles of the fertile carpels, originally united, later separate and diverge so that the adjacent bundles of two neighbouring fertile carpels come into contact and fuse into a single bundle in line with the loculi, thus giving rise to the illusory appearance that these new bundles are placental strands formed by the other (sterile) set of carpels. Styles with two vascular bundles representing half the vascular system of each of the two neighbouring fertile carpels.

**Malpighia coccifera.** Sepals with paired glands. Glands 8, 7 or 6 according as only those on sepal 3 are missing as in *Stigmaphyllon* (see above) or as the adjacent gland on one or both neighbouring sepals is also wanting. Andrœcium zygomorphic through unequal development of individual members belonging to the same whorl. G 3, sterile + 3, fertile. Styles springing from between the ovary lobes, thick, curved, often unequal as in *Tristellateia* (see above) and from the same cause. Stigmas small, terminal, oblique, concave. Fruit drupaceous.

Stamens obdiplostemonous, as in *Stigmaphyllon* (see above), and for the same reason. Sterile carpels without midrib bundles or any distinctive tract of cells in corresponding positions. Fully developed styles with two vascular bundles representing one placental strand from each of two neighbouring fertile carpels. Shorter thinner styles with only a single bundle representing a placental bundle from one carpel.



## 52. TREMANDRACEÆ

Flower ♂, actinomorphic, hypogynous. K 4 or 5 C 4 or 5 A 4 + 4 or 5 + 5 or 6–8 standing in one whorl G 2, median sterile + 2 lateral, fertile. A ring-shaped disc sometimes present between the corolla and andrœcium. Gynœceum syncarpous. Ovary bilocular. Ovules 1 or 2 in each loculus, pendulous. Style single. Stigma terminal, entire. Fruit a capsule with loculicidal or septicidal dehiscence.

## ILLUSTRATIVE TYPES

**Tetralthea spp.** (*e.g.* **T. thymifolia**). K 4, orthogonal C 4, diagonal A 6–8 in one whorl, standing singly or in pairs in front of the petals G 4, 2 median, sterile 2, lateral, fertile. Disc absent. Fruit a capsule with loculicidal dehiscence.

The vascular ground-plan of the perianth and andrœcium is altogether exceptional and provides the clue to the anomalous arrangement of the stamens. Eight trunk cords turn out from the central cylinder at the flower base. Each of the four cords on the sepal radii breaks up into three strands. The middle strand continues its outward course and becomes a sepal midrib. The two lateral strands remaining behind diverge towards the adjacent petal radius on each side and either pass into the petal intact or after a branch has been detached which becomes a stamen bundle. Hence all the stamens, their bundles being derived originally from the four antesepalous trunk cords, stand in a single ring. When only six stamens are present two stand in front of each of two petals and one in front of each of the two others, and two of the above-mentioned vascular strands in the position of the two missing stamens pass entire into the petals. When seven stamens are formed, two stand in front of each of three petals and one in front of the remaining petal, and only one of the above-mentioned strands passes entire into a petal. When there are eight stamens, two stand in front of each petal, and all the above-mentioned vascular strands give off a staminal branch before passing into a petal.

The disposition of the stamens in such a way that the members of a wholly or partially duplicated antesepalous whorl come to stand singly or in pairs in front of the petals, the antepetalous whorl proper being suppressed, together with the particular vascular scheme which underlies this arrangement are highly exceptional if not unique, though a parallel to individual features is to be found elsewhere. Duplication of the antesepalous staminal whorl accompanied by suppression of the antepetalous whorl occurs, *e.g.* in *Lawsonia* (Lythraceæ) and *Damasonium* (Alismataceæ) (see under these Families later in the present Volume, Part 8, p. 276, and Part 15, p. 538, respectively). For the converse case in which the duplicated members of the antepetalous stamen whorl stand so far apart that they give the illusory appearance of representing the antesepalous whorl which is, in fact, missing, see later in the present Volume under Cucurbitaceæ, Part 13, p. 489. Marginal veins of commissural origin in the petals are characteristic, *e.g.* of Theophrastaceæ, some Myrsinaceæ and almost all Primulaceæ, but there is no duplication in the androecium of these Families for the antesepalous stamen whorl does not usually attain separate morphological form. Since the vascular bundles for all the stamens in *Tetralthea* are derived from the same trunk cords as the sepal midribs and not independently from the central cylinder it follows naturally that the four carpels, if they constitute a single whorl, should alternate with the petals.

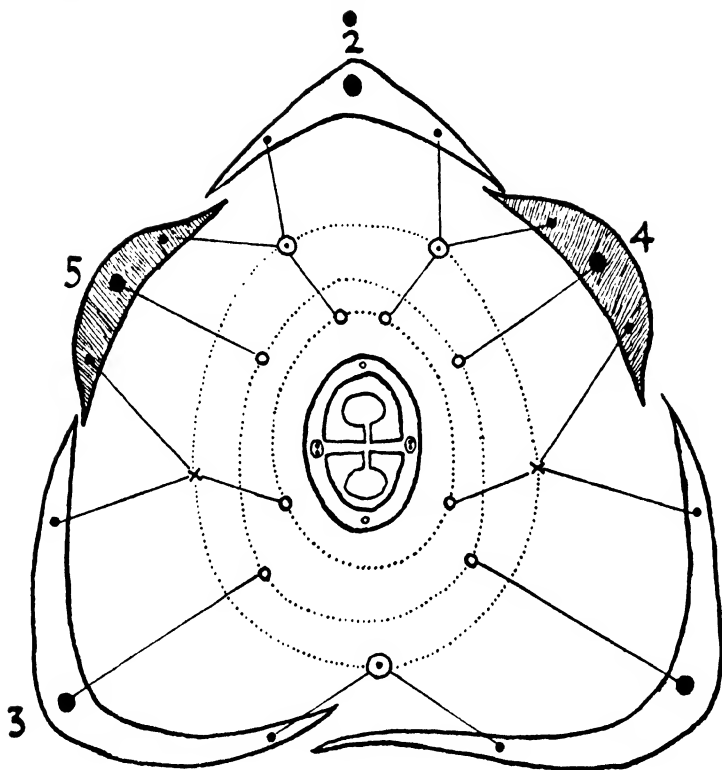
## 53. POLYGALACEÆ

Flower ♀, hypogynous, zygomorphic. Full basic ground-plan K 5 C 5 A 5 + 5 G 5, sterile + 5, fertile, but rarely, if ever, realised regularly in any one species, reduction occurring almost always in both gynæceum and andrœcium and often in the corolla. Sepals generally very unequal in size, the inner postero-lateral pair being large and petaloid and arising distinctly later than the three outer ones which are smaller and green. Only the anterior and two postero-lateral petals then generally fully developed, the antero-lateral pair, if present, being scale-like and non-vascular. In the few types in which all five petals reach full development the sepals are not markedly different in size and appearance (*e.g.* *Salomonina*, *Xanthophyllum*). Anterior petal generally boat-shaped. Stamens generally 4 + 4 through suppression of the median member in each whorl, less often 4 + 3, sometimes 4 + 1 or 4 + 0. Filaments generally monadelphous, the tube being split completely at the back. Between the andrœcium and the gynæceum glandular disc tissue forming a complete ring or developed only on the posterior radius. Gynæceum very rarely isomerous with the outer whorls, usually of 2 median, sterile and 2 lateral, fertile carpels, the ovary being then almost always bilocular, rarely unilocular through the failure of the fertile carpels to extend to the centre. Style single, straight or curved. Stigma lobes in the dimerous gynæceum, when distinct, 2, standing over the sterile carpels, often unequal and of different form. Ovules in the bilocular ovary solitary in each loculus; in the completely unilocular ovary several, in two rows on each placenta. Fruit generally a capsule dehiscing loculicidally, sometimes samaroid or nut-like.

## ILLUSTRATIVE TYPES

\***Polygala** (Milkwort). K 5, quincuncially arranged, with commissural marginal veins, the 2 outer small, the 2 inner postero-lateral large and petaloid. C 3, the two antero-lateral petals being suppressed. A 4 + 4, monadelphous. G 2 median, sterile, solid (see below) + 2 lateral, fertile, semi-solid. Ovary bilocular. Style curved flattened, with a terminal hook. Receptive stigma one, crest-like, standing over one of the sterile carpels. Centred over the other sterile carpel a spoon-shaped cavity in which the shed pollen collects. Ovules 2. Fruit a capsule, dehiscing loculicidally.

**Polygala** affords an illustration of the relation existing between a particular type of vascular ground-plan and the development of petaloid colouring in the sepals. The fact that here the manifestation of this inter-relation is affected by a time factor gives it a special interest. In most forms exhibiting this relation the flower is actinomorphic and only a single perianth whorl is present. All the members of the perianth (tepals) then become coloured (see under Sterculiaceæ, Vol. I, Part 4, pp. 114 and 118 ; also 19b, p. 204, Figs. 8 and 9 ; also earlier in the present Volume under *Chrysosplenium* (Saxifragaceæ) and *Cephalotaceæ*, Part 5, pp. 156 and 142, respectively). In *Polygala* the flower is zygomorphic. The perianth consists of two whorls, and the postero-lateral sepals, 4 and 5, are petaloid. Petaloid coloration of sepals and tepals occurs when trunk cords on the alternate (petal) set of radii do not give rise to petal midrib bundles, but are entirely used up in the formation towards the outside of commissural lateral veins for the adjacent sepals and (generally) bundles for a whorl of stamens on these radii towards the inside. In *Polygala* (as stated above) the petaloid postero-lateral pair of sepals (which though large have a narrow base) develop much later than the other three. They receive commissural lateral veins from the trunk cords on the antero-lateral, and from those on the postero-lateral petal radii. Now the cords on the antero-lateral petal radii form no petal midrib bundles for the petals on these radii are suppressed. As these cords break up they give rise first to a bundle for the superposed stamen, then to a commissural lateral for the adjacent antero-lateral sepal. After an interval the residual portion of the cords passes bodily into the adjacent postero-lateral sepal.



*Polygala myrtifolia*. The flower in transverse section (semi-diagrammatic). The sepals (numbered in order of development) and ovary are shown in outline. The petals and stamens are represented only by their vascular bundles, the successive whorls being indicated by the concentric dotted contours. The purple colour in the two inner (youngest) sepals (sepals 4 and 5) is indicated by shading. (These sepals, though larger than the outer ones, are narrower at the base.) Vascular bundles lying on the same dotted contour belong to members of the same whorl. Vascular bundles connected by continuous lines are derived from the same trunk cord. (For the probable connection between the vascular ground-plan and the coloration of the postero-lateral pair of sepals see the text.)

- |                                     |                           |
|-------------------------------------|---------------------------|
| ● Sepal midrib bundles.             | ○ Stamen bundles.         |
| ⊙ Petal midrib bundles.             | ○ Sterile carpel bundles. |
| • Sepal commissural marginal veins. | ① Fertile carpel bundles. |

x Position of the lost bundles of the two missing antero-lateral petals.

FIGURE 9.

Hence these two sepals become petaloid. The antero-lateral sepals also receive commissural laterals from these same trunk cords, but they remain green. This result would naturally follow if the petal component of the trunk cord remained behind in the residual portion when the first lateral was detached, but later, no petal being developed, passed conjoined with the later formed lateral into the postero-lateral sepal. These vascular relations are easily observed in large-flowered forms with A 8, such as *P. myrtifolia* (see Fig. 9). In small-flowered types with K 5 C 3 A 7, the origin of the anterior lateral vein in the two postero-lateral sepals is less easily traced. In these types the anterior antepetalous stamen attains development, but, on the other hand, the two stamens on the radii of the two missing antero-lateral petals are wanting. As the result of the suppression of both petal and stamen on these radii, no vascular bundle turns out from the residual central vascular system on these radii to supply the lateral to the adjacent portion of the antero-lateral sepal on one side of this radius, and of the postero-lateral sepal on the other side. These laterals spring direct from this central residual system in which it may be supposed that some elements corresponding with the missing cord still persist (though owing to the compact nature and small size of this system they cannot be identified), and that the above-mentioned laterals are derived from these elements for, as in the A 8 types, the two postero-lateral sepals are coloured.

**Salomonina.** K 5 C 3 A 4 or 5. Sepals small, nearly equal in size, without commissural marginal veins, hence the postero-lateral pair are never petaloid. Stigma punctiform.

**Muraltia** sp. K 5 C 3 A 7 (4 + 3). Sepals very slightly unequal in size, without commissural marginal veins, hence the postero-lateral pair are not petaloid.

## 54. EUPHORBIACEÆ

Flowers unisexual, monœcious or diœcious, when monœcious ♂ and ♀ usually in the same inflorescence, often greatly reduced from the full basic ground-plan, generally actinomorphic. Perianth of calyx and corolla (*e.g. Croton spp.*), more often the corolla, sometimes also the calyx, aborted or wanting. Petals when present free or united. Glandular disc structures often present. ♂ Flower. A as many, or twice as many as the sepals, or more numerous, or reduced to 1,  $\pm$  G rudiment. ♀ Flower. G generally 3, sometimes 4 or 2, rarely as many as 5–20 (*Hura*), or reduced to 1 (*Eremocarpus*), sterile + as many fertile. Ovary syncarpous, with as many loculi as sterile carpels. Styles as many as the sterile carpels and centred over these carpels; often forked above, sometimes divided almost to the base; or united for most, or for all of their length into a single hollow column with separate stigmatic lobes (*e.g. Hura*), or with a single entire stigma (*e.g. Dalechampia*). Ovules 1 or 2 in each loculus. Fruit generally dry and separating into 3 two-valved cocci through median radial splitting at first of the fertile carpels which also become torn at right angles lengthwise so as to leave a central column formed of the detached placentæ (septicidal and septifragal dehiscence), and later of the sterile carpels (loculicidal dehiscence) so that each coccus falls into two-valves. Sometimes berry-like or drupaceous.

## ILLUSTRATIVE TYPES

**\*Euphorbia spp.** (Spurge). Flowers monœcious, both sexes present in the same inflorescence. Partial (ultimate) inflorescence a cyathium (a distinctive arrangement characteristic of all genera in the section Euphorbieæ) in which a tubular involucre of 5 bracts, generally

with 5, sometimes with 4, semilunar or horned glands on its free margin alternating with the tips of the bracts, encloses 5 groups of ♂ flowers arising in the axils of reduced non-vascular bracts, and arranged round a central ♀ flower, the whole structure thus presenting a resemblance to a single ♀ flower. ♂ flowers always, ♀ almost always without perianth. Each ♂ flower reduced to one stamen borne on a separate filamentous stalk to which it is articulated by an obvious 'joint' (node). (In the allied genus *Anthostema* a small cup-shaped perianth is exerted at this level.) The ♀ flower is carried outside the involucre by a prolongation of the axis. Gynæceum trimerous (3 + 3). Ovary trilocular. Ovules solitary in each loculus, pendulous. The 3 styles, united at the base, shortly separate, each dividing sooner or later into two arms. Fruit separating into 3 cocci.

The vascular system at the base of the involucre consists of an outer ring of five cords and a second inner alternating ring of five cords of which two are weaker than the other three. Each of the five outer cords shortly breaks up to yield the midrib of the involucreal bract on the corresponding radius, the bundles for the superposed (*i.e.* axillary) group of ♂ flowers (the accompanying rudimentary bract structures being non-vascular), and a pair of bundles running at first horizontally to right and left, respectively. The adjacent horizontally running bundles derived from two neighbouring midribs later turn upwards and both enter the marginal gland intervening between these midribs. In species in which all five outer cords give off such a pair of lateral bundles, five marginal glands are formed. In those species in which two neighbouring midribs only develop such a lateral bundle on the side away from each other, only four glands are present, no gland being formed on the radius between these two midribs. In species in which the bundles entering the gland furnish a fairly symmetrical system extending, if well developed, through the width of the gland, the gland is oval. If they develop more vigorously near the margins of the gland, the gland is crescent-shaped or two-horned as in *E. Peplus*.

Of the five unequal cords forming the inner ring at the base of the involucre, the two weaker ones shortly cease to



be traceable, so that the prolongation of the axis which carries up the gynæceum has only three cords. At the ovary base a portion of each of the three cords turns outwards to become a sterile carpel midrib. The residual portions are organised into the midribs and placental bundles of the three alternate fertile carpels forming the septa. These latter midribs shortly divide into two preparatory to septicidal dehiscence in the fruit. At a higher level the sterile carpel midribs similarly divide into two, thus facilitating the eventual loculicidal dehiscence of the separate cocci which then split into two valves.

The fertile carpel bundles come to an end at the top of the ovary, the twin bundles of the sterile carpel midribs alone being continued into the style column and on into the arms of the three forked or deeply split separate styles.

The presence at the base of the involucre of an inner ring of five vascular cords of which only three persist to serve the gynæceum indicates that the  $G\ 3 + 3$  ground-plan of existing forms has arisen by reduction from  $G\ 5 + 5$ . This interpretation receives support from the fact that the  $G$  rudiment in the ♂ flowers of some types is sometimes pentamerous (e.g. *Dicella*).

**\*Mercurialis** (Dog's Mercury). Flowers dioecious, rarely monœcious, the ♂ in clusters along the elongated flowering axes, the ♀ 1-3 together on shorter axes. ♂ Flower.  $K\ 3\ C\ 0\ A\ 8-20\ G\ 0$ . ♀ Flower.  $K\ 3\ C\ 0\ A\ 2$  staminodal  $G$  (generally) 2, sterile + 2, fertile. Styles 2, united below, separating above, remaining entire, stigmatic down their inner face. Ovules and fruit as in *Euphorbia* (see above).

**Ricinus communis** (Castor-oil). Flowers monœcious and occurring in the same compound inflorescence, the ♂ occasionally with a rudimentary gynæceum. ♂ Flower.  $K\ 3-5\ C\ 0\ A\ \infty$  in numerous bundles through repeated branching of the primordia which arise in a series of rings. ♀ Flower.  $K\ 3-5$ , caducous  $C\ 0\ G\ 3$ , sterile + 3, fertile. Ovary trilocular. Ovules solitary in the loculi. Styles 3, united below, separating above and then standing over the sterile carpels, each deeply split into two stigmatic arms. Fruit falling into 3 cocci through median radial splitting of the fertile carpels. Each coccus eventually falls into two valves through median radial splitting of the sterile carpels.

Sepals with true lateral veins. Sterile carpels with midrib bundles, but the fertile carpels are without separate midrib bundles. The placental bundles come to an end at the ovule level so that only the three sterile carpel midribs are prolonged into the style column. One midrib bundle passes into each individual style where it shortly divides into two in accord with the bifurcation at a higher level into two stigmatic arms.

## 55. CALLITRICHACEÆ

Flowers unisexual and monœcious, solitary in the axils of the leaves, subtended by a pair of lateral, membranous, non-vascular bracteoles, the ♀ below, the ♂ above; or the ♂ two or more in series on a reduced axillary shoot; without perianth. ♂ Flower A 1. ♀ Flower G 4, 2 lateral sterile, 2 median fertile. Ovary bilocular but appearing quadrilocular through the intrusion into the loculi of the midrib tissue of the sterile carpels. Ovules 4, 2 in each loculus, pendulous. Styles 2, centred over the sterile carpels, stigmatic along their length. Fruit finally separating into 4 nut-like segments through median radial splitting of all the carpels.

## ILLUSTRATIVE TYPES

**\*Callitriche.** See the characters of the Family.

Analysis of the floral ground-plan is rendered difficult by the extreme degree of reduction. From analogy with the Euphorbiaceæ it may be inferred that the single stamen of the ♂ flower is probably the surviving member of an original whorl of two, and is not, therefore, to be considered as terminal on the axillary axis, an inference which receives support from the fact that a terminal growing point can sometimes be distinguished. In the ♀ flower the only differentiated vascular bundles present in the ovary are the twin placental bundles of each fertile carpel, midrib bundles being absent from both sets of carpels in this region. But as the loculi close, two fine strands representing the sterile carpel midribs make their appearance and pass, respectively, into the two styles.

## 56. BUXACEÆ

Flowers unisexual, generally monœcious, those of both sexes then in the same inflorescence, the ♂ below, the ♀ above, rarely diœcious, actinomorphic. Perianth present or absent, when present always single. ♂ Flower. A 4 (2 + 2) (see below) or numerous, rarely 5, ± G rudiment. ♀ Flower always without staminodes. G (generally) 3, sterile + 3, fertile. Ovary syncarpous. Styles free or connate at the base. Ovules 2 or 1 in each loculus. Fruit a capsule dehiscing loculicidally through median radial splitting of the sterile carpels, or drupaceous.

## ILLUSTRATIVE TYPES

**\*Buxus sempervirens** (Box). Flowers monœcious. ♂ Flower. T 4 (2 lateral + 2 median) A 4 (2 lateral + 2 median) + G rudiment. ♀ Flower hypogynous. T variable A 0 G 3, sterile + 3, fertile. Ovary trilocular becoming unilocular above as the fertile carpels fail to reach the centre. Ovules 2 in each loculus. Styles 3, centred over the sterile carpels. Alternating with the styles protuberances inclined towards the centre, formed of the apical parenchyma of the fertile carpels. Stigmas furrowed, zygomorphic. Fruit a capsule, dehiscing loculicidally.

In the ♂ flower the two vascular bundles for the outer pair of lateral tepals turn out from the central cylinder earlier than those for the inner median pair, hence the bundles for the four stamens which originate independently also turn outwards in two successive pairs. Alternation of successive dimerous whorls thus accounts for the position of the outer stamens on the radii of the outer tepals and of the inner stamens on the radii of the inner tepals.

In the ♀ flower three vascular bundles turn outwards from the centre to become the midribs of the sterile carpels. The vascular elements remaining behind in the centre become organised on the alternate radii into the placental bundles

of the fertile carpels which are without separate midrib bundles. At the summit of the ovary the twin placental bundles of each fertile carpel diverge and come to lie alongside the neighbouring sterile carpel midrib on each side. The ground tissue of these carpels, nevertheless, remains undivided—a very exceptional feature. The parenchyma in the middle line between the twin placental bundles forms the protuberances above-mentioned, alternating with the styles. Each style receives the whole vascular system of a sterile carpel and half the system of the fertile carpel on each side, and thus represents one whole carpel and a portion of the fertile carpel on each side, a construction in accord with the form of the stigma.

## 57. EMPETRACEÆ

Flowers generally unisexual and diœcious, often with rudiments of the non-functional sex, exceptionally monœcious or ♀ (*Empetrum*), actinomorphic, with tri- or dimerous whorls in the perianth and andrœcium. G 2-9, sterile + 2-9, fertile. Ovary with as many loculi as sterile carpels. Style single, very short. Stigmas as many as the sterile carpels and standing over these carpels. Ovules solitary in the loculi. Fruit a drupe with 2-9 'stones.'

## ILLUSTRATIVE TYPES

**\*Empetrum** (Crowberry). Flowers generally unisexual and diœcious, rarely ♀. ♂ Flower. K 3 C 3 A 3, antesealous. ± G rudiment. ♀ Flower. K 3 C 3 G 6 (-9), sterile + 6 (-9), fertile. ♀ Flower generally K 3 C 3 A 3, less often K 3 C 3 A 3 + 3, G as in the ♀ flower.

Reconstruction in the residual vascular cylinder above the level of origin of the perianth and stamen bundles permits of a change of ground-plan with formation of carpels of the outer whorl on all the primary construction radii or even on additional radii, and of the whorl of alternate fertile carpels on a new set of radii. Sterile carpels with, fertile carpels without, midrib bundles. Only the sterile carpel midrib bundles are prolonged into the style, the plascental bundles of the fertile bundles coming to an end at the ovule level.

## 58. CORIARIACEÆ

Flower generally ♂, hypogynous, in its fullest development isomerous throughout and then actinomorphic.  $K\ 5\ C\ 5\ A\ 5 + 5$ , diplostemonous  $G\ 5$  antesepalous + 0, or 5 antesepalous + 5 (or fewer) antepetalous. Gynæceum apocarpous. Styles distinct, thick, papillose over the whole surface except at the extreme base and along the dorsal mid-line. Ovules solitary in each ovary, pendulous from the top of the loculus. Fruits achene-like, partly enclosed by the petals which become enlarged and fleshy.

The diplostemonous condition obtains whether the flower is five-whorled ( $G\ 5 + 0$ ) or six-whorled ( $G\ 5 + 5$ ) since the apocarpous condition prevents the setting up, even in flowers with two carpel whorls, of that state of congestion which is envisaged as resulting in the outer carpels being developed on the petal radii with consequent obdiplostemony (see Vol. I, Introduction, p. 8; also 28, p. 299). In these radial relations of the whorls *Coriaria* presents an exact parallel with *Xanthorrhiza apiifolia* (see under Ranunculaceæ, Vol. I, Part 2, p. 36; also 28, *loc. cit.*). [*Xanthorrhiza*, like *Coriaria*, has ordinarily pentamerous whorls, but on p. 299 in the latter account through a clerical error, they are represented as hexamerous.]

The vascular bundles for the several whorls turn out from the central cylinder independently. In flowers with  $G\ 5 + 0$  residual undifferentiated vascular elements remaining in the centre above the level of delimitation of the five carpel midribs give evidence of the loss of a second carpel whorl. The carpels are of the typical valve type, the placental strand being given off from the carpel midrib and lying on the same radius as the midrib. Only the midrib is prolonged into the style.

## ILLUSTRATIVE TYPES

**Coriaria myrtifolia.** See the characters of the Family.

## 59. ANACARDIACEÆ

Flowers ♂, or unisexual through abortion, generally slightly syngonous, rarely almost hypogynous. Very rarely isomerous throughout (commonly in *Buchanania*). Calyx and corolla actinomorphic, isomerous, generally with 5-, less often with 4- or 3-merous whorls. Andræcium in one or two whorls usually isomerous with the perianth whorls, but sometimes through abortion with fewer stamens than petals, sometimes with more than twice this number. Some members sometimes sterile. Gynæceum always zygomorphic through infertility of all carpels except one, almost always oligomerous and syncarpous, in *Buchanania* (probably) pseudo-apocarpous (see below). Ovary sometimes multilocular, more often unilocular. Ovule always solitary. Styles distinct or more or less connate; when distinct standing over the sterile carpels; with terminal stigmas or with elongated lobes papillose along the inner face. Fruit dry or drupaceous, 1-seeded.

## ILLUSTRATIVE TYPES

**Buchanania.** Flower ♂. K 5 C 5 A 5 + 5 G 5 (or 4 or 6) antepetalous, sterile + 1, antesepalous, fertile. Gynæceum pseudo-apocarpous (see below). Ovule 1. Styles distinct. Stigmas terminal, oblique. Fruit drupaceous, with a thin outer wall and hard endocarp.

The vascular bundles for the stamens turn out from the central cylinder independently, some elements being left behind in the centre on each of the corresponding radii. The feeble development of these residual elements and the asymmetry introduced by the great difference in size between the one fertile and the four sterile ovaries render it difficult to determine with certainty the complete carpel ground-plan. One of the central strands on a petal radius becomes the dorsal bundle of the large fertile ovary and is clearly a carpel midrib. The strands on the other petal radii shortly cease to be traceable, the four small sterile ovaries being without



a differentiated dorsal bundle. They are also without placental bundles, ovule rudiment and loculus but show a radial line of characteristic conducting cells on the ventral side which open to the surface as the ovaries become free and channelled on the ventral face.

The two placental bundles of the fertile ovary are not derived as in monocarpellary ovaries from the dorsal midrib, but are organised, apparently, from part of the residual strand lying on the neighbouring sepal radius on each side. The above facts point to the conclusion that the form of the gynæceum is the result of reduction from a full ground-plan of  $G\ 5 + 5$ ; that four of the inner carpels no longer attain morphological form, being represented by vascular elements which no longer serve the ovaries to which they properly belong; that the four small sterile ovaries may therefore be regarded as monocarpellary; that the fertile ovary is formed of  $\frac{1}{2} \ 1 \ \frac{1}{2}$  carpels. This interpretation is in accord with the ground-plan of the other genera in the Family. The distinctive feature of *Buchanania* on this view is not, as the outward appearance suggests, that it has an apocarpous gynæceum of monocarpellary ovaries; but that there has been no reduction in the number of carpels of the outer whorl such as has occurred in other members of the Family.

**Pistacia** (e.g. *P. Lentiscus*, *P. vera*) (Pistachio-nut). Flowers dioecious. Perianth single or lacking. ♂ Flower.  $T\ 1$  or  $2\ A\ 3-5$ . ♀ Flower.  $T\ 2-5\ G\ 3$ , sterile +  $1$  actually (? also  $2$  more potentially) fertile. Ovary unilocular. Ovule borne on the wall of the ovary near the base. Style single. Stigma lobes  $3$ , standing over the sterile carpels, elongated, papillose on their inner face. Fruit with a thin outer wall and hard endocarp.

The feebly developed vascular system of the ovary makes it difficult to determine whether the two non-ovule-bearing carpels of the inner fertile whorl should be regarded as present or as completely lost.

**Rhus spp.** (Sumach). Flowers polygamous. ♀ Flower.  $K\ 5\ C\ 5\ A\ 5 + 0$ , of which  $1-4$  are often sterile.  $G$  as in *Pistacia* (see above). Ovary unilocular. Ovule basal. Styles  $3$ , distinct or more or less connate. Stigmas capitate. Fruit drupaceous.

**Mangifera** (Mango). Flowers polygamous. ♂ Flower. K 5 C 5 A 5 + 5 or 5 + 4-0, only 1-4 being generally fertile, the rest being more or less aborted; sometimes all fertile when A = 5 + 0. G as in *Pistacia* (see above). Ovule basal. Style single. Stigma entire. Fruit drupaceous.

**Schinus molle**. Flowers polygamous and dioecious. ♂ Flower. K 5 C 5 A 5 + 5. G as in *Pistacia* (see above). Ovary unilocular. Ovule pendulous from near the top of the loculus. Styles distinct. Stigmas capitate. Fruit drupaceous.

## 60. AQUIFOLIACEÆ

Flowers unisexual but with rudiments of the non-functional sex, dioecious or sometimes polygamous, actinomorphic, hypogynous, five-whorled, the whorls generally isomerous throughout, regularly alternating and 4- or 5-merous. K 4 or 5 C 4 or 5 A 4 or 5 G 4 or 5, sterile, antepetalous, + 4 or 5, fertile, antesepalous; or G 3 or 6-8, sterile + 3 or 6-8, fertile. Disc absent. Gynæceum syncarpous. Ovary generally with as many loculi as fertile carpels through union of these carpels in the centre. Style absent or very short and stout, formed of all the carpels and receiving the vascular systems of the fertile as well as of the sterile carpels, hence its thickness. Stigma terminal, lobed or capitate. Ovules 1 or 2 in each loculus. Fruit a drupe with as many 1-seeded 'stones' as loculi.

## ILLUSTRATIVE TYPES

**\**Ilex aquifolium*** (Holly). Flowers polygamous or dioecious. K 4 or 5 C 4 or 5 A 4 or 5 G 4 or 5, sterile + 4 or 5, fertile. Stigmas sessile, as many as the loculi and centred over them. Ovules solitary in the loculi, pendulous.

The whorls alternate throughout, since only five are present, and since the vascular bundles for each whorl originate independently. Sepals with true lateral veins arising simultaneously with the midrib from the central cylinder.

## 61. CELASTRACEÆ

Flowers ♂ or unisexual with rudiments of the non-functional sex, sometimes diœcious, actinomorphic, hypogynous, five-whorled. Perianth and andrœcium isomerous, generally 4- or 5-merous. K 4 or 5 C 4 or 5 A 4 or 5 in regular alternation. Disc present lining the base of the corolla and surrounding the ovary. Stamens borne on the disc. G 2-5, sterile + 2-5, fertile. Gynœceum syncarpous. Ovary with 2-5 complete or incomplete loculi according as the fertile carpels fuse in the centre or, even though they may come into contact, remain free on the inner face. Style single, generally short. Stigma capitate or lobed with as many lobes as sterile carpels and standing over these carpels. Ovules generally 2 in each loculus, rarely 1 or numerous. Fruit a capsule, with loculicidal dehiscence through median splitting of the sterile carpels or indehiscent; or a berry or drupe.

## ILLUSTRATIVE TYPES

**\*Euonymus europæa** (Spindle-tree). K 4 or 5 C 4 or 5 A 4 or 5 G 4 or 5, sterile antepetalous + 4 or 5, fertile, antesepalous. Ovary sunk in the disc. Style very short. Stigma lobes as many as the sterile carpels. Fruit a capsule with loculicidal dehiscence. Seeds solitary.

The whorls alternate throughout since only five whorls are present and the vascular bundles for each whorl originate independently. Sepals with true lateral veins.

## 62. ACERACEÆ

Flowers ♀, or sometimes structurally but more often functionally unisexual through a varying degree of abortion, very rarely through complete suppression of one sex. When ♂ through a high degree of abortion of the gynæceum they soon wither and fall; when the gynæceum, though infertile, is less reduced, they may remain for some time. Hypogynous, or perigynous in the ♂. Usually pentamerous with an oligomerous gynæceum.  $K\ 5\ C\ 5$  or sometimes wanting  $A\ 5 + 5$  or rarely  $5 + 0\ G\ 2$ , fertile, generally either median or slightly inclined to the median plane. In functionally ♀ flowers the anterior and posterior median stamens are frequently suppressed. A ring-shaped glandular disc with undifferentiated vascular strands is usually present, being extra-staminal in hypogynous, intra-staminal in perigynous species. Ovary bilocular, with two pendulous ovules in each loculus. Styles two. Fruit of two, winged, one-seeded mericarps (samaras) which hang suspended from a bifurcate prolongation of the axis. (For a similar development of the axis in Umbelliferæ see later in the present Volume, Part 8, p. 310.)

Flowers with  $G\ 3$  are not unusual, while occasionally one may be formed with  $G\ 4$  or even  $G\ 5$ . These facts indicate that the dimerous gynæceum of the type is the result of reduction from a pentamerous ground-plan. For although such pleiomery in the gynæceum is sometimes accompanied by an increase in the number of members in the outer whorls, this is not always so. It may occur in flowers otherwise of normal construction.

The bilocular condition of the ovary is not due to fusion of the carpel margins, but is brought about by a prolongation of the axial ground tissue which completes

the transverse partition. In the fruiting stage this tissue becomes sclerosed and affords a rigid support for the mericarps.

All but one species in the Family belong to the genus *Acer* (Sycamore, Maple).

### ILLUSTRATIVE TYPES

**\**Acer* spp.** (including **\**A. campestre*** (Maple) and **\**A. pseudoplatanus*** (Sycamore)). Flowers ♂ and ♀, monœcious. For the ground-plan see the account of the Family.

***A. Negundo*** (Ash-leaved Maple). Flowers unisexual and diœcious, apetalous. ♀ Flower often with G 3 and even G 4. For further details see the account of the Family.

The ♀ flower of this species affords particularly favourable material for examination of the vascular ground-plan of the gynœceum owing to the absence of corolla, andrœcium and disc.

## 63. HIPPOCASTANACEÆ

Flowers polygamous, ♀ and ♂, monœcious, the two forms occurring in the same inflorescence, ♀ below, ♂ (which usually have a rudimentary gynæceum) above, hypogynous, zygomorphic with oblique symmetry, the plane of symmetry passing through the postero-lateral sepal 4. (For the order of development of the sepals in the quincuncial calyx see earlier in the present Volume under Saxifragaceæ, Part 5, p. 149, Fig. 7.) Full ground-plan of the perianth and andrœcium K 5 C 5 A 5 + 5, but the anterior petal sometimes aborted or suppressed and the total of stamens commonly 7 through suppression of three members of the antesepalous whorl standing in line with the three neighbouring sepals 1, 4, 2, respectively; sometimes 8, or reduced further to 6 or 5. Within the corolla an extra-staminal annular disc. Gynæceum of 3 sterile + 3 fertile carpels. Ovary trilocular through union of the fertile carpels in the centre. Style single. Stigma terminal, undivided. Ovules 2 in each loculus. Fruit a leathery capsule, dehiscing loculicidally through median radial splitting of the sterile carpels.

The vascular bundles for the stamens turn out from the central cylinder independently; when only five develop they appear usually (? always) to represent a complete antesepalous whorl.

## ILLUSTRATIVE TYPES

\**Æsculus Hippocastanum* (Horsechestnut). See the characters of the Family.

## 64. SAPINDACEÆ

Flowers markedly polygamous, *viz.* ♂ with a rudimentary gynæceum, apparently ♀ but with closed anthers and non-functional pollen, ♀ but generally with rudiments of the andrœcium, the different forms occurring on the same individual and frequently in the same inflorescence, less often on different individuals, hypogynous, actinomorphic or zygomorphic with oblique symmetry as in Hippocastanaceæ (see under that Family earlier in the present Volume, Part 6, p. 224). Ground-plan of the perianth and andrœcium generally either K 5 C 5 A 5 + 5, but K sometimes 6 or 7, sometimes simulating reduction to 4 through union of two neighbouring sepals (3 and 5 in the order of development) and A sometimes ∞; or K 4 C 4 A 5 + 4. Disc extra-staminal, annular or unilateral and then centred in the plane of symmetry and superposed upon sepal 4. Stamens in flowers based on a pentamerous ground-plan very generally reduced to 8 through suppression of those superposed, respectively, on sepals 1 and 2, more rarely to 7 or 6, exceptionally to 5, representing the complete antesepalous whorl; but sometimes > 10. G 3 (4 or 2), sterile + 3 (4 or 2) fertile. Ovary syncarpous with 3 (4 or 2) loculi, sometimes becoming unilocular above as the fertile carpels fail to extend to the centre. Ovules solitary in the loculi, or two or more. Style single, generally terminal, less often sunk more or less deeply between the loculi. Stigmatic lobes when separate centred over the sterile carpels. Fruit various.

## ILLUSTRATIVE TYPES

**Xanthoceras sorbifolium.** Flower actinomorphic. K 5 C 5 A 8 (3 + 5) G 3, sterile + 3, fertile. Disc of 5 antesepalous horn-like structures. Style short, ending



in three erect stigma lobes. Ovules several, in two rows in each loculus. Fruit a capsule, dehiscing loculicidally through median radial splitting of the sterile carpels.

**Ungnadia speciosa.** Flower zygomorphic. K 5 C 5, or 4 through suppression of the petal lying in the plane of symmetry of, and opposite to, sepal 4 A 8 (3 + 5) G 3, sterile + 3, fertile. Disc unilateral. Ovary stipitate. Ovules 2 in each loculus. Style filamentous. Stigma terminal, punctiform, slightly trifid. Fruit a capsule dehiscing as in *Xanthoceras* (see above).

**Cardiospermum.** Flower zygomorphic. K 5, or 4 through fusion of sepals 3 and 5 C 4 through suppression as in *Ungnadia* (see above). Disc unilateral. Ovary excentric, sometimes sessile, sometimes stipitate A 8 (3 + 5) excentric G 3, sterile + 3, fertile. Ovules solitary in each loculus. Style very short, ending in three diverging stigma lobes. Fruit a thin-walled, bladder-like capsule, opening in different ways.

## 65. RHAMNACEÆ

Flower ♂, seldom polygamous, still more rarely dioecious and then generally with rudiments of the non-functional sex, actinomorphic, more or less syngonous, K 5 or 4 C 5 or 4 or sometimes wanting A 5 or 4, always antepetalous G generally 2-4, sterile + 2-4, fertile, when dimerous the sterile carpels median, the fertile lateral; in forms isomerous throughout the sterile carpels and loculi always antesepalous. Gynæceum syncarpous. Ovary generally with as many loculi as fertile carpels but unilocular in a few forms in which these carpels do not extend to the centre. Style single, rarely wanting. Stigma lobes when distinct as many as the sterile carpels and standing over these carpels. Ovules generally solitary, rarely 2 in one or more of the loculi. Disc tissue in various forms usually present between the andrœcium and gynæceum. Fruit dry, falling into one-seeded dehiscent or indehiscent segments, or drupaceous with several 'stones,' or dry and indehiscent.

## ILLUSTRATIVE TYPES

**\*Rhamnus** (Buckthorn). Flowers ♂ or polygamous and dioecious, slightly syngonous, the perianth-stamen tube lined at the base with disc tissue. Fruit drupaceous with 2-4 'stones.'

**\*R. Frangula**. Branches without thorns. Flower ♂. K 5 C 5 A 5 G 2-3, sterile + 2-3, fertile.

**\*R. cathartica**. Branches often with thorns. Flowers polygamous and dioecious. ♂ Flower. K 4 C 4 or petals sometimes wanting A 4. ♀ Flower. K 4 C 4 or petals sometimes wanting G 4, sterile, antesepalous + 4, fertile, antepetalous. Stigmas distinct.

Sepals with commissural marginal veins. Petal midribs and stamen bundles being derived from the same trunk cords suppression of the corolla does not affect the radial position of the stamens which remain on the petal radii. Formation of the sterile carpels on the sepal radii is in the above circumstances in accord with the normal scheme of alternation, since the sterile carpel midribs alternate with the petal-stamen, trunk cords. Hence these carpels occur on the sepal radii even when the corolla is suppressed.

## 66. VITACEÆ

Flowers ♂, polygamous, or diclinous and monœcious or dioecious, hypogynous, actinomorphic. Generally K 4 or 5 C 4 or 5 A 4 or 5, or rarely with as few as 3 or as many as 7 members in each whorl. Stamens always antepetalous. Filaments generally free from one another and from the corolla, rarely forming a tube joined at the base with the corolla (*Leea*). Between andrœcium and gynœceum a plainly or obscurely lappeted ring-shaped disc rarely completely fused with the ovary, or more or less separate glands. G generally 2, sterile + 2, fertile, rarely 3-6 sterile + 3-6 fertile (*Leea*). Gynœceum syncarpous. Ovary usually with, or appearing to have as many loculi as fertile carpels through union or only contact of these carpels in the centre. Ovules 1 or 2 in each loculus. Style single, thick and short or long and filamentous. Stigma terminal, undivided or 2-lobed, in forms with G 4 + 4 4-lobed. Fruit generally a 2-celled berry, seldom 1-celled or 3-8-celled (*Leea*), with 1 or 2 seeds in each cell.

The vascular bundles of the stamens do not originate independently but arise conjoined with the petal midrib bundles, hence as in the nearly allied Family Rhamnaceæ (see earlier in the present Volume, Part 6, p. 228) they are always antepetalous.

## ILLUSTRATIVE TYPES

**Parthenocissus spp.** (*e.g.* *Ampelopsis*, Virginia Creeper). Flower ♂. K in the form of a simple rim or sometimes 5-toothed C 5 A 5, free from the corolla, G 2, sterile + 2 fertile. Ovary appearing bilocular but the fertile carpels often merely in contact in the centre without becoming fused. Style short, thick. Stigma

entire. Ovules 4. Disc completely fused with the ovary. Fruit a 1-4 seeded berry.

Sepals with true lateral veins. Style formed from all the carpels, receiving the vascular systems of the fertile as well as those of the sterile carpels, hence its thickness.

**Vitis vinifera** (Grape Vine). Flowers polygamous and dioecious. K in the form of a simple rim or sometimes five-toothed, C 5, adhering together and falling in the bud stage as a hood-shaped structure A 5, free from the corolla. Ovary as in *Parthenocissus* (see above). Style very short and thick. Stigma undivided. Disc in the form of more or less separate glands. Fruit as in *Parthenocissus* (see above).

## Part 7

### Dicotyledons

Family	67.	Dilleniaceæ
„	68.	Ochnaceæ
„	69.	Guttiferæ
„	70.	Dipterocarpaceæ
„	71.	Elatinaceæ
„	72.	Tamaricaceæ
„	73.	Frankeniaceæ
„	74.	Cistaceæ
„	75.	Bixaceæ
„	76.	Flacourtiaceæ
„	77.	Passifloraceæ
„	78.	Loasaceæ
„	79.	Datisceæ
„	80.	Begoniaceæ
„	81.	Cactaceæ
„	82.	Thymelæaceæ
„	83.	Elæagnaceæ



## 67. DILLENiaceæ

Flower ♂, or rarely polygamous or dioecious, hypogynous, actinomorphic. Calyx and corolla generally pentamerous (K 5 C 5). Ground-plan of the andrœcium also generally pentamerous but rarely in the form A 5 + 5 as in *Hibbertia salicifolia*. The antepetalous whorl generally suppressed. The antesepalous whorl then represented by  $> 5$  stamens owing to multiplication (e.g. *Hibbertia glaberrima* A  $5_3 + 0$ , *H. tetrandra* A  $5_4 + 0$ , *H. perfoliata*, *Tetracera* (*Hibbertia*) *volubilis* A  $5_\infty + 0$ ); all fertile or some staminodal; in a regular ring when the gynœceum is central, grouped partly or wholly to one side if the gynœceum is excentric and then sometimes oligomerous through suppression. Gynœceum rarely syncarpous (e.g. *Actinidia*, *Dillenia* spp., *Davilla*, spp.), generally pseudo-apocarpous through median radial splitting of the fertile carpels from within outwards or from without inwards (see below). Carpels sometimes isomerous with the perianth whorls (in pentamerous types 5, antepetalous, sterile + 5 antesepalous, fertile) and central; or oligomerous (3-1, sterile + 3-1, fertile) and then sometimes central, sometimes excentric; or pleio-merous (*Hibbertia* spp., *Actinidia* spp.). Ovaries when several more or less free or when single, if formed of only two carpels (one sterile, one fertile), unilocular; when single and composed of  $> 2$  carpels multilocular, with as many loculi as sterile carpels. Styles as many as the sterile carpels and centred over these carpels, generally wholly free, rarely connate for a longer or shorter distance, terminal or springing below the top from the back of the ovaries, generally channelled on the ventral face towards the apex. Stigmas terminal; as commonly when formed of one valve carpel or of  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels grooved on the ventral



face, and hence symmetrical only about the median plane. Ovules generally numerous in 2-several rows in each loculus. Fruits when dry dehiscing down the ventral suture or in the dorsal mid-line; when baccate indehiscent.

Sepals generally with commissural marginal veins. In types with antesepalous groups of stamens, the antesepalous vascular cords serving these groups break up into numerous branches after they have turned out from the central cylinder, hence these stamens are whole stamens. Single styles generally with one vascular cord formed of the sterile carpel midrib with which is fused half the vascular system of the fertile carpel on each side.

Median radial splitting of the fertile carpels occurs from without inwards when the central parenchyma of the axis extends upwards sufficiently far for the fertile carpels to be attached to it by their ventral face at the base after they have become free on their dorsal face from the surrounding perianth-stamen tissue; from within outwards when the axis parenchyma ceases below the level at which the carpels become disjoined from the outer whorls. A radial split also occurs, as commonly, in the free ovary of two carpels, one sterile, one fertile (see *e.g.* earlier in the present Volume under Leguminosæ, Part 5, p. 184), and in the partially free ovaries of  $\frac{1}{2}$  +  $\frac{1}{2}$  carpels when exposed on the ventral face. This cleavage takes place between the twin placental strands of the whole fertile member in the former case and between the adjacent placental strands of neighbouring halved fertile carpels in the latter case. The loculus thus comes to communicate with the exterior until the cleft is closed as the surfaces bordering the opening which have remained in contact become reunited.

### ILLUSTRATIVE TYPES

**Tetracera (Hibbertia) volubilis.** K 5 C 5 A 5. + 0 G 5, sterile + 5, fertile. Gynæceum pseudo-apocarpous,

the fertile carpels splitting from without inwards. Fruit dry.

**Hibbertia tetrandra.** K 5 C 5 A 5<sub>4</sub> + 0 G 5, sterile + 5, fertile. Gynæceum pseudo-apocarpous, the fertile carpels splitting from the free ventral face outwards. Fruit dry.

## 68. OCHNACEÆ

Flower ♂, hypogynous, almost always actinomorphic. Calyx and corolla generally pentamerous (K 5 C 5). Corolla almost always contorted. Andræcium seldom in two isomerous whorls and all fertile (5 + 5), frequently  $\infty$  and then rarely all fertile, more often one whorl of 5 alone fertile, the rest staminodal. When 5 + 5 diplostemonous if the carpels are arranged in one whorl, the flower being then five-whorled; it is diplostemonous also when the carpels are in two whorls and the flower is six-whorled if the gynæceum is borne on a prolongation of the axis (gynophore) (see Vol. I, Introduction, p. 8). Gynæceum apocarpous in the region of the ovaries, the whole number of carpels (sometimes 5 but often 10 or more) standing in a single whorl and all fertile; or syncarpous, the carpels being arranged in two whorls (5 + 5 or 3 + 3), the inner whorl alone being fertile. In the apocarpous forms the several ovaries are monocarpellary, unilocular and contain a single ovule. In the syncarpous gynæceum the single ovary is multilocular or unilocular according as the fertile carpels extend to the centre or not. Styles connate, a rare condition in a gynæceum truly apocarpous in the region of the ovaries, sometimes separating at the summit. Stigmas then as many as the loculi, and centred over them. In apocarpous gynæcea the stigmas, if separate, are zygomorphic, as commonly when derived from a single valve carpel. Fruit drupaceous or baccate, or a capsule dehiscing septicidally through median radial splitting of the fertile carpels or indehiscent.

In the arrangement in *Ochna* and its nearest allies of separate monocarpellary ovaries in a single whorl comparison may be made with *Cephalotus* (see earlier in the present Volume, under Cephalotaceæ, Part 5, p. 142).

But in the latter genus the broad summit of the floral axis is so shaped that the ovaries are from the outset disjoined on the ventral face from the central parenchyma, and the styles are distinct. In *Ochna* the central parenchyma of the axis tapers to an end above the closed loculi and the styles remain conjoined into a hollow column, a central cavity replacing the central parenchyma.

### ILLUSTRATIVE TYPES

**Ochna spp.** (e.g. *O. Kirkii*). K 5 C 5 A  $\infty$ , all fertile G 10 (or more or fewer) arranged in a single ring. Ovaries separate, each of one carpel and containing one ovule. Styles connate, separating above into a corresponding number of stigma-bearing branches. Stigmas zygomorphic. Individual fruit a drupe.

The vascular units which serve the calyx break up into numerous strands below the exertion level, hence each sepal receives in place of a midrib bundle a 'fan' of separate strands. The residual vascular system, as seen in transverse section, consists of a five-pointed star. Elements situated at the points of the star give rise to the petal midrib bundles. Residual vascular strands at the periphery of the star turn out irregularly and breaking up further serve the numerous stamens irregularly arranged in rings. The central elements of the star become consolidated into (generally) ten bundles, each of which furnishes a carpel midrib and placental strand lying on the same radius.

**Sauvagesia spp.** (e.g. *S. erecta*). K 5 C 5 A 5<sub>x</sub> in the form of filamentous staminodes + 5 broad staminodes + 5 fertile stamens G 3, sterile + 3, fertile, syncarpous. Ovary trilocular at the extreme base becoming unilocular as the central parenchyma of the axis comes to an end and the fertile carpels fail to reach the centre. Style single. Stigma simple and entire. Ovules  $\infty$ , in two rows on each fertile carpel. Fruit a capsule, dehiscing septicidally through median radial splitting of the fertile carpels.

The vascular system serving the andrœcium consists at first of five compound units on the sepal radii. These units become resolved into (a) branches extending to right and left

which serve an outer ring of  $\infty$  thread-like staminodes ; (b) five vascular bundles which turn tangentially and take up a position on the petal radii to serve a second whorl of five broad antepetalous staminodes with two very unusual features, an excentric, almost marginal, midrib and contorted præfloration ; (c) the bundles of a third whorl of five fertile antesepalous stamens.

## 69. GUTTIFERÆ

(Hypericoideæ, Clusioideæ and Calophylloideæ)

Flower generally ♂, actinomorphic, hypogynous, five-whorled through absence of an antesealous stamen whorl; sometimes polygamous or diœcious. Ground-plan generally pentamerous (rarely tetramerous) in the perianth and andrœcium, with an isomerous or oligomerous gynœceum. Corolla contorted. Stamens generally numerous through multiplication of the antepetalous members; filaments free, or united into antepetalous bundles, or all soldered together. Gynœceum syncarpous. Ovary multilocular or unilocular according as the fertile carpels meet, or fail to meet in the centre. Fruit a capsule dehiscing septicidally or loculicidally through median radial splitting in the former case of the fertile, in the latter of the sterile carpels; or a berry.

Of the six sections into which the Family is divided (Kielmeyeroideæ, Hypericoideæ, Endodesmioideæ, Calophylloideæ, Clusioideæ, Moronoboideæ) only Hypericoideæ, which includes the single genus abundant outside the tropics, *viz.* *Hypericum* (6†, 28†, and 33), Clusioideæ and Calophylloideæ are considered.

## HYPERICOIDEÆ-HYPERICEÆ

Flower ♂. Antesealous stamen whorl entirely suppressed. The numerous stamens, arising from multiplication of the antepetalous members, free or united into antepetalous bundles. Ovary unilocular or multilocular. Styles distinct. Fruit a capsule dehiscing septicidally or a berry.

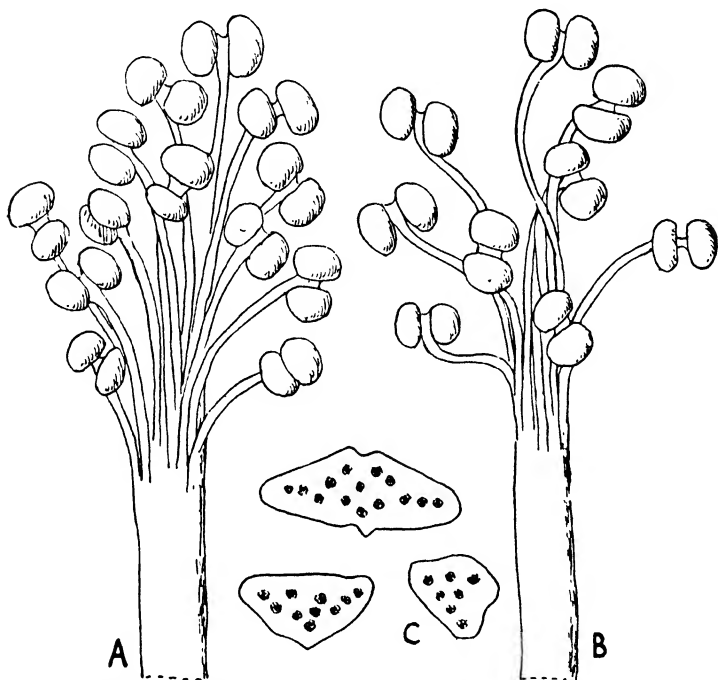
*Hypericum* (St. John's Wort) (6, p. 303, Figs. 5, 6; 28, pp. 313-321, Figs. 16-33, and 33, pp. 160-163). Plant usually with abundant oil glands. Flower generally

K 5 C 5 A 0 + 5<sub>x</sub> G 5, sterile + 5, fertile or 3, sterile + 3, fertile. Sterile carpels and loculi, when 5, antesepalous. Calyx quincuncial (for this arrangement see under Saxifragaceæ earlier in the present Volume, Part 5, p. 149, Fig. 7). Sepals with commissural marginal veins, sometimes unequal in size, 1 and 2 being similar and larger, 4 and 5 similar and smaller, and 3 of intermediate size. These relations naturally lead to unequal spatial conditions on the different radii, differences which in the smaller-flowered species affect the position of the staminal vascular bundles. Stamens in the larger-flowered species  $\infty$ , in five approximately equal bundles with the filaments almost or quite free; in the smaller-flowered species less numerous, in one small single and two larger unequal double bundles, each of the latter resulting from the fusion of two bundles (see Fig. 10).

In species with a triadelphous andrœcium the single bundle occurs on the radius on which the greatest amount of space is available, *viz.* between sepals 1 and 3, the larger double bundle in the sector of sepal 4 and the smaller double bundle in the sector of sepal 5. The filaments in each bundle are united for a longer or shorter distance. The ovary in species with five separate bundles of stamens is pentamerous or trimerous; in species with a triadelphous arrangement always trimerous. [For the evidence that *H. peplidifolium* constitutes no exception to this latter statement, see 33, *loc. cit.*]

The superposition of the five bundles of stamens upon the petals is explained by the fact that the vascular component for each antepetalous staminal member arises from the same trunk cord as the corresponding petal midrib bundle. This component is detached in all species from each of these five trunk cords, but owing to the unequal amount of intervening space on the five alternate (sepal) radii fusion takes place between the staminal

vascular units lying on each side of the radius of sepal 5 and also, though with occasional exceptions, between those lying on each side of sepal 4 in those species which



*Hypericum aegypticum* (a species with a triadelphous andrœcium). A. One of the two double bundles of stamens. B. The single bundle from the same flower. C. The three bundles of stamens from another flower in transverse section; the larger double bundle (top) with 14 vascular bundles, the smaller double bundle (left) with 10 vascular bundles, the single bundle (right) with 7 vascular bundles. The number of vascular bundles = the number of stamens in the bundle. (From 28, p. 318, Figs. 32, 33.)

FIGURE 10.

are characterised by three bundles of stamens but which may, in an occasional flower, show four bundles. Hence the appearance in normal flowers of these species that two antepetalous staminal members have been suppressed is illusory.



Reduction in the gynæceum of some species having five separate bundles of stamens from a pentamerous to a trimerous ground-plan is on the other hand genuine, following, as it does, a process of reconstruction in the central vascular cylinder after the organisation of the sepal commissural marginal+petal midrib+antepetalous stamen trunk cords. The three carpels in each whorl of the trimerous gynæceum being equidistant do not in consequence correspond with any three carpels in the corresponding whorls of the pentamerous gynæceum. When a tri-radiate arrangement has been brought about in the andrœcium, as described above, the new scheme of symmetry is always continued in the gynæceum, species with a triadelphous andrœcium having invariably a trimerous gynæceum (see above).

**Ascyrum.** Perianth tetramerous.  $K_4$ , orthogonal, in two pairs  $C_4$ , diagonal. The arrangement is exceptional, the lateral pair being the outer, the median, the inner.

#### CLUSIOIDEÆ-CLUSIÆ

Flowers diœcious, rarely ♀ or polygamous. ♂ Flower. Staminal filaments free or all soldered together, never in antepetalous bundles. ♀ Flower. Stigmas sessile, distinct, centred over the sterile carpels. Fruit a capsule generally dehiscent septically through median radial splitting of the fertile carpels and also septifragally.

#### CALOPHYLLOIDEÆ

Flowers ♀ or polygamous. Stamens  $\infty$ , free or united only at the base. Style single, long. Fruit fleshy, indehiscent.

### ILLUSTRATIVE TYPES

#### HYPERICOIDEÆ-HYPERICÆ

**\*Hypericum calycinum.**  $A_{5x}$ , numerous, in equal bundles. Styles 5. Ovary unilocular. Fruit a capsule.

**\*H. Androsæmum** (Tutsan). A  $5_x$ , numerous, in equal bundles. Styles 3. Ovary unilocular. Fruit a berry.

**\*H. perforatum**, **\*H. quadrangulum**. A  $3_x$ , numerous, in unequal bundles (one single, two double). Styles 3. Ovary trilocular. Fruit a capsule.

**\*H. humifusum**. A  $3_x$ , rather few in unequal bundles (one single, two double). Styles 3. Ovary trilocular. Fruit a capsule.

**\*H. Elodes**. (6, p. 303, Figs. 5, 6), A  $3_x$ , very few in unequal bundles (one single, two double). With 3 bilobed disc structures on the intervening radii. Styles 3. Ovary unilocular. Fruit a capsule.

#### CLUSIOIDEÆ-CLUSIÆ

**Clusia**. ♂ Flower. A  $\infty$ , free or all more or less united. G rudimentary or absent. ♀ Flower. Stamens present or absent. Ovary multilocular. Capsule leathery or fleshy.

The multilocular ovary of *C. flava* (and of other species of the genus) furnishes one of a few examples in which the radial boundaries of the carpels are plainly defined. The fertile carpels appear in transverse section as narrow radial sheets of tissue extending outwards to the surface between the sterile carpels and enlarging towards the centre when the placenta are continuous with the parenchyma of the axis. Their position is indicated on the ovary surface by distinct furrows. Dehiscence of the capsule takes place in the line of these carpels (septicidally), and they also become torn lengthwise at right angles to their radial face (septifragally). With the result that each valve of the fruit is bordered on each margin by an inwardly directed flange representing the split half of the peripheral portion of the neighbouring fertile carpel on each side, the central portion remaining attached to the central seed-bearing column formed of the placenta.

Though not precisely paralleled by either, the gynæceum in *Clusia* presents certain points of resemblance to those of *Impatiens* and of *Gossypium*. In *Impatiens noli-me-tangere*, an exceptional genus with three carpel whorls (see under Balsaminaceæ in Vol. I, Part 3, p. 82), the carpels of the

second whorl, as in *Clusia*, appear in transverse section as thin radial sheets of tissue bounding the loculi laterally and extending outwards to the surface between the carpels of the outer whorl. Being a little broader than those of the corresponding carpels in *Clusia* they give rise to a double contour line, each being defined externally by a furrow on each side. Furthermore, when the fruit splits these carpels become torn lengthwise, the peripheral portion remaining attached as a flange to the carpels of the outer whorl while the central portion remains conjoined with the central seed-bearing column. In *Gossypium* in which the ovary, at least from near the base upwards, is composed of a single whorl of semi-solid fertile carpels, the radial boundaries of these members become defined as the alternate sterile carpels of a separate whorl cease to persist between them (see under Malvaceæ in Vol. I, Part 4, p. 110). For another instance of the visible definition of carpel boundaries, see also under Pittosporaceæ, Part 5, p. 159. Although radial demarcation of the carpels is rare, indication of their boundaries on the surface of the ovary is less uncommon. It is characteristic of many Cruciferae (well seen in the glabrous forms of *Matthiola*) and of some Papaveraceæ (e.g. *Glaucium*).

#### CALOPHYLLOIDEÆ

**Calophyllum.** Flowers polygamous. Sepals and petals together 4-12, not always distinct from one another. Ovary unilocular with a solitary basal ovule. Stigma large, shield-shaped or funnel-shaped.

## 70. DIPTEROCARPACEÆ

Flower ♂, actinomorphic, generally hypogynous. Outer whorls pentamerous but often with multiplication of the antepetalous stamen whorl ( $K\ 5\ C\ 5\ A\ 5 + 5_2-\infty$ ). Calyx valvate or quincuncial (see earlier in the present Volume, p. 149, Fig. 7). Corolla contorted. Gynæceum generally trimerous ( $G\ 3$ , sterile + 3, fertile). Ovary trilocular, sometimes becoming unilocular above as the fertile carpels fail to reach the centre. Ovules 2 in each loculus. Styles almost always connate, only with rare exceptions (*e.g.* *Anisoptera*) as many as the sterile carpels. Stigma terminal, undivided or lappeted. Fruit a 1-seeded nut, generally enclosed in the persistent enlarged calyx with which it may be partially coherent. All the sepals sometimes becoming prolonged upwards in the fruiting stage. In types with a quincuncial calyx sometimes only sepals 1 and 2 or sepals 1, 2 and 3 becoming enlarged.

The vascular bundles for the stamens turn out from the central cylinder independently. Those for the antesepalous members remain undivided. Those for the antepetalous members also remain undivided in  $A\ 5 + 5$  types. But in those with  $> 10$  stamens they break up into as many strands as there are stamens in the antepetalous groups. Thus, when 15 stamens are present ( $A\ 5 + 5_2$ ), as in the section *Shoreæ*, the antepetalous stamen bundles divide radially in two. But owing to the inequilateral shape of the petals as the result of torsion the two stamens representing each antepetalous staminal member do not stand symmetrically in front of each petal, but so much to one side that one of the two comes to appear to be antesepalous in origin. Hence the illusory appearance that the stamens arise in three whorls ( $A\ 5 + 5 + 5$ ).

## ILLUSTRATIVE TYPES

**Shorea spp.**  $K\ 5$ , quincuncial. Sepals 1, 2 and 3 larger than sepals 4 and 5.  $C\ 5\ A\ 5 + 5_2\ G\ 3$ , sterile + 3, fertile. All the sepals enlarged in the fruiting stage, three being much larger than the other two.

**Hopea spp.** Flower as in *Shorea* (see above). Only sepals 1 and 2 enlarged in the fruiting stage.

## 71. ELATINACEÆ

Flower ♂, actinomorphic, hypogynous, generally isomeric throughout, usually six-whorled, rarely five-whorled through suppression of the antepetalous stamen whorl. When six-whorled diplostemonous, the bundles for the outer and inner stamens arising conjoined with the sepal and petal midrib bundles, respectively. Ovary multilocular. Loculi in line with the sepals. Styles and stigmas distinct, centred over the sterile carpels. Fruit a capsule with septicidal and septicifragal dehiscence.

Since the vascular bundles for the staminal whorls do not arise independently, the suppression of the antepetalous whorl in some species does not affect the radial position of the succeeding whorl, hence the sterile carpels are antesepalous in all species (28, pp. 300, 301).

## ILLUSTRATIVE TYPES

**\*Elatine Hydropiper, E. Alsinastrum.** K 4 C 4 A 4 + 4 G 4, sterile, antesepalous + 4, fertile, antepetalous.

**\*E. hexandra.** K 3 C 3 A 3 + 3 G 3, sterile, antesepalous, + 3, fertile, antepetalous.

**E. triandra.** K 3 C 3 A 3 + 0 G 3, sterile, antesepalous + 3, fertile, antepetalous.

**Bergia suffruticosa.** K 5 C 5 A 5 + 5 G 5, sterile, antesepalous + 5, fertile, antepetalous.

**B. ammannioides.** K 5 C 5 A 5 + 0 G 5, sterile, antesepalous + 5, fertile, antepetalous.

## 72. TAMARICACEÆ

Flower almost always ♂, hypogynous, actinomorphic, six-whorled, or five-whorled through the suppression sometimes of the antesepalous, sometimes of the antepetalous stamen whorl. When five-whorled through suppression of the antepetalous stamens isomerous throughout (many species of *Tamarix*, *Reaumuria*); when reduced through loss of the antesepalous stamen whorl with an oligomerous gynæceum (*Fouquieria*). When six-whorled always with an oligomerous gynæceum (some species of *Tamarix*, *Myricaria*). When the antepetalous stamen whorl alone is present the normal number of stamens is usually increased by multiplication (*Fouquieria*, *Reaumuria*). Ovary unilocular throughout or multilocular below and becoming unilocular above as the fertile carpels no longer meet in the centre. Styles sometimes distinct, sometimes connate, sometimes centred together with the stigmas over the sterile carpels, sometimes over the fertile carpels ('commissural'). Fruit a capsule dehiscing loculicidally through median radial splitting of the sterile carpels.

## ILLUSTRATIVE TYPES

**\**Tamarix* spp.** (e.g. *T. tetrandra*) (Tamarisk). K 4 (2 outer lateral, 2 inner median) C 4, diagonal A 4, orthogonal, exserted on the outer face of a crenate ring-shaped disc + o G 4, diagonal, of valve form, sterile + 4, orthogonal, solid, fertile. Ovary unilocular throughout. Ovules more than 2 abreast on the placentæ. Style single below, giving rise above to four stigmatic arms centred over the sterile carpels.

The vascular bundles for the antesepalous stamens turn out from the central cylinder independently, those for the antepetalous stamens, when present, arise conjoined at first with the petal midrib bundles (e.g. *T. octandra*). Hence in

A 4 + 4 as in A 4 + 0 species the sterile carpels and loculi are antepetalous, and the andrœcium in the eight-stamened species obdiplostemonous. The single style receives twelve vascular bundles, and each of the four stigmatic arms three of these bundles, representing a sterile carpel midrib with a primary pair of laterals.

**Myricaria germanica.** K 5 C 5 A 5 + 5, monadelphous, exerted externally to a ring-shaped disc, diplostemonous G 3, solid, sterile + 3, semi-solid, fertile. Ovules more than two abreast on the placentæ. Stigmas centred over the fertile carpels ('commissural').

The vascular bundles for both stamen whorls turn out from the central cylinder independently, but since the carpel whorls are oligomerous, the conditions which lead to obdiplostemony are not set up and the staminal whorls alternate regularly with the perianth whorls.

**Reaumuria spp.** K 5 C 5 A 0 + 5<sub>∞</sub> G 5, sterile + 5, fertile. The petal midribs, the bundles for the phalanges of stamens and the sterile carpel midribs are all derived from the same delimited vascular units, hence petals, phalanges, outer carpels and loculi all lie on the petal radii. Ovary multilocular below becoming unilocular above. The tissue of the fertile carpels is so thin and so delicate at the points at which the partitions spring from the outer wall of the ovary that it is easily ruptured so that these carpels come later to consist of two portions, an outer portion forming part of the wall of the ovary and the radial plate of tissue forming the 'septum' which appears as a loose thin lamina only attached at the base and in the centre up to the level at which the ovary remains multilocular. In this tearing of the fertile carpels into an outer and an inner portion, *Reaumuria* resembles those Caryophyllaceæ having ovaries multilocular at the base and unilocular above (see under that Family in Vol. I, Part 4, p. 101).

**Fouquieria splendens.** K 5 C 5 A 0 + 5<sub>3</sub> G 3, sterile + 3, fertile. Stamen vascular bundles carried out from the central cylinder conjoined with the petal midrib bundles, hence the triplets of stamens are antepetalous. At the base of each filament is a blunt, finger-like process similar to that occurring in some species of *Oxalis*, though in *Fouquieria* it occurs on the inner face of the filaments and in *Oxalis* on the outer face of the antesealous members (see under Oxalidaceæ in Vol. I, Part 3, p. 73).

## 73. FRANKENIACEÆ

Flowers ♂, rarely polygamous, actinomorphic, hypogynous. K 4-7, gamosepalous C 4-7 A (generally) 3 + 3, monadelphous for a short distance G (generally) 3, sterile + 3, fertile. Gynæceum syncarpous. Ovary unilocular. Ovules borne on the ovary wall in the lower part of the loculus; when numerous more than two abreast on each fertile carpel. Style single below, separating above into as many filaments as there are sterile carpels, the filaments being centred over these carpels and stigmatic down their inner face. Fruit a capsule dehiscing loculicidally through median radial splitting of the sterile carpels.

## ILLUSTRATIVE TYPES

**Frankenia lævis** (Sea Heath). K 5 C 5 A 3 + 3 G 3, sterile + 3, fertile.

Sepals with true lateral veins. Petals with a basal scale-like ligule. The vascular bundles for the stamens turn out independently from the central cylinder. The transition from a pentamerous perianth to a trimerous andrœcium represents a genuine reduction in the floral ground-plan and also, following a process of reconstruction, in the vascular ground-plan. Herein *Frankenia* differs from those species of *Hypericum* having a pentamerous perianth and three bundles of stamens, the appearance of reduction in the floral ground-plan in the latter genus being illusory and without change in the vascular ground-plan (see earlier in the present Volume under Guttiferæ, Part 7, p. 240).



## 74. CISTACEÆ

Flower ♂, hypogynous, actinomorphic, generally five-whorled through absence of an antepetalous stamen whorl. Usually pentamerous throughout with multiplication of the five staminal members (K 5 C 5 A 5<sub>x</sub> G (generally) 5, sterile, antepetalous + 5, fertile, antesepalous (26†)). Frequently with apparent reduction in the number of sepals through partial or complete fusion of some members. Sometimes with actual reduction in the corolla, andræcium or gynæceum through a change of ground-plan. Very rarely with a pleiomerous gynæceum (G 10, sterile + 10, fertile). Sepals with quincuncial præfloration in the bud (for this arrangement see earlier in the present Volume under Saxifragaceæ, Part 5, p. 149, Fig. 7), generally with commissural marginal veins. Corolla contorted. Ovary multilocular or unilocular according as the fertile carpels meet, or fail to meet, in the centre. Style single, of varying length and thickness, sometimes almost lacking. Stigmas sometimes distinct, more often continuous, surmounting both sterile and fertile carpels. Fruit a capsule dehiscing loculicidally, through median radial splitting of the sterile carpels, rarely also septifragally through the tearing of the fertile carpels.

The vascular system of the fertile carpels comes to an end at the top of the ovary, but the sterile carpel midribs are prolonged into the style and continue up to the stigmas, bifurcating just below this level, sometimes anastomosing, sometimes remaining separate.

In having a one-whorled polyadelphous andræcium, Cistaceæ resembles some sections of the Guttiferæ (*e.g.* Hypericoideæ), but differs from the latter Family in that the single staminal whorl is alternipetalous and in that the loculi when isomerous lie on the petal radii. The different radial position of both stamens and loculi follows naturally from the different vascular fusions (different constitution of the trunk cords), for the successive whorls of vascular units always alternate in both Families. In *Hypericum*, where the

staminal vascular bundles arise fused with the petal midrib bundles, the five groups of stamens are naturally antepetalous (see under Guttiferæ earlier in the present Volume, Part 7, p. 240). In Cistaceæ, where the staminal vascular bundles turn out from the central cylinder independently, they and the corresponding groups of stamens lie on the sepal radii. Since the formation of the sterile carpel vascular bundles follows directly upon that of the stamen bundles it naturally results that they and the loculi will be antesepalous in *Hypericum* and antepetalous in Cistaceæ. It is to be noted, however, that owing to the torsion of the corolla and the inequilateral shape of the petals the line of the petal midrib does not coincide with the true petal radius which must be visualised as lying midway between the stamen radii.

For the development of the petal midrib bundles from the junction points of branches from the antesepalous trunk cords, see 26†.

### ILLUSTRATIVE TYPES

**Cistus** (26, pp. 47-57, Figs. 1-12). Plant rich in gum resin. Sepals 1 and 2 usually as large as, less often smaller than, the other three. Style long, slender and geniculate (with a knee-shaped bend), or long, straight and of medium thickness, or very short and thick. Stigmas generally forming a hemispherical or dome-shaped top to the style, appearing 'commissural' when viewed from above, but in reality continuous over both sterile and fertile carpels, though so thrown into folds that the stigmatic surface of the sterile carpels is only visible from the side or from below.

**Cistus spp.** (almost all). G 5 + 5.

**C. ladaniferus.** G (full ground-plan) 10 + 10.

**\*Helianthemum vulgare** (Rock-rose) (26, pp. 57-64, Figs. 13-25, 33-36). Sepals 1 and 2 small. G 3 + 3. Style long, geniculate. Stigmas as in *Cistus*, but those of the sterile carpels much smaller in proportion to those of the fertile carpels than in the latter genus.

## 75. BIXACEÆ

Flower ♀, actinomorphic, hypogynous.  $K\ 4$  or  $5\ C\ 4$  or  $5\ A\ \infty$  through multiplication of the antesepalous members  $G\ 2-5$ , sterile +  $2-5$ , fertile. Stamens generally free, rarely united in bundles at the base. Gynæceum syncarpous. Ovary unilocular or partially or completely multilocular according to the extent to which the fertile carpels protrude into the ovarian cavity. Ovules  $\infty$ , in several rows on each placenta. Style single. Stigma terminal; when lobed the lobes are centred over the fertile carpels ('commissural'). Fruit a capsule dehiscing loculicidally into  $2-5$  valves.

## ILLUSTRATIVE TYPES

**Bixa Orellana** (16, p. 87†).  $K\ 5\ C\ 5\ A\ \infty\ G\ 2$ , median, sterile + 2, lateral, fertile. Calyx imbricate. Sepals with large vascular glands on the exposed margins, *i.e.* with a pair on each of the sepals 1 and 2 and with one on sepal 3. Stamens mostly free to the base. Ovary unilocular (*loc. cit.*, Figs. 18-20).

The vascular bundles for the andræcium turn out from the central cylinder independently, one on each sepal radius. These primary bundles break up and divide further in their course to the exertion level. The residual vascular elements serving the gynæceum form a complete cylinder. Two bundles turn out from this cylinder in the median plane to become the midrib bundles of the sterile carpels. The large alternate arcs become 'condensed' into two placental bundles and branches derived from them which spread over all the intermediate radii.

## 76. FLACOURTIACEÆ

Flowers generally ♂, sometimes polygamous and then monœcious or diœcious, cyclic or rarely hemicyclic, actinomorphic, hypogymous or partially syngonous, very rarely completely syngonous. Perianth of calyx and corolla, or uniseriate and cyclic, or exceptionally acyclic (*e.g. Berberidopsis*, 16†). When distinguishable into calyx and corolla the petals more numerous than the sepals and without any symmetrical relation to them (*e.g. Oncoba*, 16†), or as many as the sepals and alternating with them, or in 2 alternating isomerous whorls. Disc structures of various forms often present within the corolla at the base. Stamens usually  $\infty$ , often in bundles alternating with the tepals in types with a single perianth, in front of the petals in types with calyx and corolla. Sometimes when not in bundles in two whorls, rarely in one whorl alternating with the tepals (*e.g. Azara microphylla*), when more numerous appearing to be irregularly arranged. Filaments rarely more or less monadelphous.

Gynæceum almost always unilocular, of 3-5 (or more or fewer) sterile carpels + 3-5 (or more or fewer) fertile carpels. Ovules generally numerous, rarely few or solitary on each placenta. Styles distinct as many as the sterile carpels and centred over these carpels, or connate with as many separate stigmas. Fruit baccate, or drupaceous, or a capsule, or dry and indehiscent with several seeds.

In genera having a single perianth whorl, vascular bundles, in addition to the midrib bundles, generally turn out from the central cylinder on the radii alternating with the tepals. Although these bundles are often feebly developed the tepals of types in which they occur give evidence of this commissural development (as in forms where the tepals are furnished with strong commissural marginal veins) by their colour being either yellowish-green (*e.g. Idesia*) or more markedly petaloid (*e.g. Latia*).

## ILLUSTRATIVE TYPES

**Berberidopsis corallina.** (16, pp. 88, 89, and Figs. 21-29). Flower ♂, hemicyclic, hypogynous. Perianth coloured. T 9-15 A 7-10 G 3, sterile + 3, fertile. Ovary unilocular. Style single. Stigmas 3, centred over the sterile carpels, each corresponding with  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels.

The residual vascular tissue supplying the gynæceum is organised into six equidistant bundles representing the midrib bundles of the six carpels. A placental branch is given off from each of the three bundles belonging to the fertile carpels. At the summit of the style the vascular system of each fertile carpel becomes divided in half. Each stigma lobe receives the whole vascular system of a sterile carpel and half the system of the neighbouring fertile carpel on each side and thus corresponds with  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels. Fruit a capsule.

**Oncoba** (16, p. 89 and Figs. 30-35). Flowers polygamous, monœcious or diœcious, cyclic, hypogynous. K 3-5 C 4-10 A ∞ G 2-10, sterile + 2-10, fertile. Ovary unilocular. Style single. Stigmas 2-10, centred over the sterile carpels. Fruit a capsule.

**Azara spp.** (e.g. *A. microphylla*, *A. Browneæ*, *A. integrifolia*) (16, p. 89). Flower ♂, cyclic, hypogynous. T 4 or 5 A 4 or 5 + 0 (*microphylla*); or 4 or 5<sub>x</sub> + 4<sub>x</sub> or 5 (*Browneæ*, *integrifolia*) G 3, sterile + 3, fertile. Style single. Stigmas 3, centred over the sterile carpels. Fruit baccate.

The last two species cited above afford examples where, although petals are absent, vascular bundles turn out from the central cylinder on both sets of radii. Those on the tepal radii became the tepal midribs. Those on the alternate radii break up. One portion, which in other types forks to furnish commissural marginals, here comes to an end as the tepals separate; the remaining portion breaks up into as many strands as there are stamens in the corresponding group.

**Idesia spp.** (e.g. *I. polycarpa*). Flowers diœcious or polygamous. T (generally) 5 C 0. Tepals petaloid.

## 77. PASSIFLORACEÆ

Plant generally with tendrils. Flowers ♂, or unisexual and then generally diœcious, rarely monœcious, usually with, rarely without, rudiments of the other sex, hypogynous, actinomorphic almost always five-whorled through absence of an antepetalous stamen whorl, isomerous throughout and generally pentamerous (K 5 C 5 (or sometimes wanting) A 5 G 5, sterile + 5, fertile) or more often with an oligomerous gynæceum (K 5 C 5 (sometimes wanting) A 5 G 3, sterile + 3, fertile) (7, p. 621† and 16, p. 104†). Outgrowths of the axis of varied form (= corona) usually present between corolla and andrœcium. The ovary generally raised considerably above the preceding whorls by the development of a gynophore. Gynophore or ovary often surrounded by an annular disc. Andrœcium sometimes conjoined for a longer or shorter distance with the gynophore (= androgynophore, a construction also occurring in some Capparidaceæ, see under that Family in Vol. I, Part 2, p. 57). Ovary unilocular. Ovules in 2-several rows on each fertile carpel. Styles as many as placentæ, separate throughout or conjoined below, centred over the sterile carpels. Stigmas terminal. Fruit a berry; or a capsule opening loculicidally, or irregularly, or (rarely) remaining closed.

## ILLUSTRATIVE TYPES

**Passiflora** spp. (Passion Flower). (7, p. 621 and p. 618, Fig. 219; 16, p. 92 and p. 104, Diagram 5). K 5 C 5 A 5 G 3, sterile + 3, fertile. Androgynophore present. Styles 3. Fruit a berry.

## 78. LOASACEÆ

Flower ♂, actinomorphic, generally completely syngonous. Perianth whorls pentamerous or tetramerous. Stamens rarely only equal in number to the sepals or to both perianth whorls, generally  $\infty$  through multiplication in one or both whorls. Gynæceum isomerous with the outer whorls, or with a reduced number of carpels. The antesepalous staminal whorl often staminodal. Ovary unilocular. Ovules rarely solitary, or few on each placenta, generally  $\infty$  in numerous rows. Style single. Stigma entire or lobed. Fruit indehiscent or dehiscing by valves which are sometimes straight, sometimes wound spirally.

## ILLUSTRATIVE TYPES

**Blumenbachia insignis** (16, pp. 92-95, with Figs. 44-55). Flower completely syngonous. K 5 C 5 A 5, staminodal + 5 G 5, antepetalous, sterile + 5, antesepalous, fertile. Ovules  $\infty$ . Styler canal as seen in transverse section with a scalloped outline, opening directly upwards to the exterior. Stigma not enlarged. Fruit spirally wound, splitting along the lines of junction of the perianth members and superposed carpels into 10 segments, each segment corresponding with an entire perianth member and the superposed carpel. This unusual method of dehiscence by the separation of whole members is paralleled in certain Orchidaceæ (e.g. *Miltonia*, *Leptotes*) in which also the flower is completely syngonous and the ovary unilocular (see under this Family in Vol. I, Part 4, p. 92).

The vascular system immediately below the flower consists of a ring of ten cords. Elements detached from these cords at the flower base turn inwards and become organised on the sepal radii into the placental bundles of the fertile carpels. As the central parenchyma of the axis comes to an end the

loculus makes its appearance, and the fertile carpels, now free on their inner face, project far into the ovarian cavity but never form complete septa. The further break-up of these ten cords into their components takes place towards the top of the ovary, the sterile carpel midrib bundles being detached first from the cords on the petal radii which then break up further into the petal midribs and antepetalous stamen bundles, the fertile carpel midrib bundles being similarly detached from the cords on the sepal radii which then break up further into the sepal midribs and antesepalous staminode bundles. Both sterile and fertile carpel midrib bundles are prolonged into the style. Before reaching the stigma level, the sterile carpel midrib bundles divide in two. Each convex sector in the outline of the canal is furnished with three vascular bundles representing the midrib bundle of a fertile carpel flanked on each side with half the vascular system of a sterile carpel. Hence these sectors are 'commissural' and correspond with  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels.



## 79. DATISCACEÆ

Flowers unisexual and diœcious or rarely polygamous, actinomorphic or nearly so. ♂ Flower. K 4-9, gamosepalous or free and unequal C 4-9 or 0, A 4-9, antesepalous or more numerous and without relation to the sepals, without trace of the gynœceum. ♀ Flower syngonous. K 3-8, becoming free above the ovary C 0 A 0 G (?) 0 + 3-8 (see below). Ovary unilocular. Styles 4-8 with enlarged terminal stigmas, or stigmas sessile, filamentous, in 3-5 pairs. Ovules  $\infty$ , in several rows on the placentæ. Fruit a capsule, opening above between the styles or tearing down the sides.

## ILLUSTRATIVE TYPES

**Datisca cannabina** (16, pp. 107, 108, and p. 106, Diagram 9). Flowers diœcious, sometimes polygamous. ♂ Flower K 4-9 C 0 A 8- $\infty$  G 0. ♀ Flower. K 3-5 C 0 A 0 G (?) 0 + 3-5, semi-solid, fertile (see below). Stigmas in 3-5 pairs, filamentous. Fruit a membranous capsule, opening above between the pairs of stigmas.

The vascular ground-plan at the flower base consists in the ♀ of a vascular cord at each of the angles and one in the mid-line of each of the intervening flat sides. The bundles at the angles become the sepal midribs. Those in the middle of the sides become the placental bundles of a corresponding number of fertile semi-solid carpels. At the summit of the ovary the placental bundles divide in two; the resulting twin strands diverge, one passing into the adjacent stigma standing at the neighbouring angle on one side, the other similarly into the adjacent stigma on the other side. Hence the pair of stigmas at each angle do not represent a single split sterile carpel but the halves of two different fertile carpels ( $\frac{1}{2} \frac{1}{2}$ ). The gynœceum thus presents a parallel with that of *Begonia* (see later in the present Volume under Begoniaceæ, Part 7, p. 260). Both exhibit the unusual feature of being composed of a single whorl of semi-solid fertile carpels. The mode of formation of the stigmas is the

same in both. There is evidence also that in *Datisca*, as in *Begonia*, an outer (in *Datisca* antesepalous) sterile carpel whorl has disappeared. For in some flowers one of the sepals, which are ordinarily unequal, may be so reduced that the corresponding vascular bundle does not enter the exerted portion but turns inwards towards one of the two superposed stigma filaments. This suggests that the bundles on the sepal radii may once have been trunk cords supplying the sepal mid-ribs and a now vanished whorl of sterile carpels. In this feature *Datisca* furnishes a parallel with *Gossypium*, in which genus also there is some evidence that a whorl of sterile carpels has become almost entirely suppressed (see under Malvaceæ in Vol. I, Part 4, p. 110).

## 80. BEGONIACEÆ

Inflorescence generally consisting of successive dichasial cymes. Flowers unisexual, normally without trace of the other sex (see under *Begonia* among Illustrative Types), monœcious, the two sexes occurring often, but not invariably, in the same partial inflorescence and then usually in definite positions in regard to one another, either with a single petaloid perianth (*Begonia*) or with calyx and corolla (*Hillebrandia*, *Begoniella*). ♂ Flower. Perianth when single petaloid, of 2 opposite free members or of 4 free members in two alternating dissimilar pairs (*Begonia*); when double differentiated into calyx and corolla, the sepals and petals free (*Hillebrandia*) or conjoined (*Begoniella*). Stamens generally  $\infty$ , rarely 4 (*Begoniella*). ♀ Flower completely syngonous with a single zygomorphic perianth of 2-5 (or more) free, unequal members and a winged ovary (most *Begonia spp.*) or incompletely syngonous with a double, actinomorphic perianth and ovary without wings (*Hillebrandia*). Ovary multilocular, or sooner or later becoming unilocular as the fertile carpels become disjoined in the centre. Fertile carpels and styles generally 2 or 3 (most *Begonia spp.* 3†, 4†, 7† and 16†), sometimes 5 (*Hillebrandia*, 16††), rarely 6 (a few *Begonia spp.*). Styles free or conjoined below, generally deeply bifurcate above. Stigmatic papillæ generally in the form of a continuous band wound spirally round the two forks, rarely terminal. Ovules  $\infty$ , in many rows on each placenta. Fruit generally a horny capsule, in syngonous *Begonia spp.* splitting near the wings, in *Hillebrandia* between the styles; rarely fleshy (*Begonia baccata*).

## ILLUSTRATIVE TYPES

**Hillebrandia sandwicensis** (16, pp. 99-107 and Figs. 56-59, and p. 104, Diagram 8).

♂ Flower. K 4 or 5 C 4 or 5 A ∞. ♀ Flower. K 5 C 5 G 5, sterile + 5, fertile. Ovary free above, without wings, multi-locular at the base but shortly becoming unilocular. Styles 5, centred over the loculi. Each style corresponds to  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels (see below).

Five vascular cords on the sepal radii furnish the sepal midribs and sterile carpel midribs, the cords becoming resolved into their two components at the level of exsertion of the calyx. Corresponding cords on the petal radii give rise to sepal commissural laterals and petal midribs. The placental bundles of the fertile carpels are delimited at the flower base. At the summit of the ovary the placental system of each fertile carpel divides in half, half the system coming to lie alongside the adjacent sterile carpel midrib on each side. Hence each style receives the vascular systems of  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels.

**Begonia.** Inflorescence generally a compound dichasial cyme, the terminal flower ♂ the laterals ♀.

**Begonia baccata.** ♂ Flower. T 2 A ∞. ♀ Flower. T 2 G generally 5 or 6 (rarely 4), sterile + 5 or 6 (rarely 4), fertile. Styles 5 or 6 (rarely 4). Fruit baccate.

Owing to branching of the vascular bundles forming the residual ring after the exsertion of the perianth and their complex anastomoses, the presence of the outer sterile whorl of carpels, though scarcely to be doubted, is less easily established than in *Hillebrandia* (see above).

**Begonia spp.** in general (3, p. 151, and Fig. 59; 4, p. 183, and Figs. 9, 10; and 16, p. 104, Diagram 7), e.g. **B. Dregei**, which offers particularly favourable material for microscopic examination owing to the simple vascular system (7, pp. 621–623, and Figs. 220 A, B, C). ♂ Flower. T 2 A ∞. ♀ Flower. T 5 G 0 + 3, semi-solid, fertile. Styles 3. Fruit dry.

The ovary in the bulk of the species thus shows as a constant characteristic the same rare condition as *Gossypium* among Malvaceæ (see under that Family in Vol. I, Part 4, p. 110) in which a like but more complete reduction from the full ground plan of two isomerous and pentamerous whorls has finally resulted in an ovary

composed of a single whorl in which the carpels are all fertile and semi-solid.

In a few forms ♂ flowers are occasionally produced with a reduced number of stamens and an ovary which is then free and usually open at the top (7, p. 618, Figs. 221, 222). ♀ Flowers, with a free, unwinged ovary having four or five fertile carpels and styles, and thus similar to that of the normal flowers of *B. baccata*, but with the ovary usually open at the top, also occur exceptionally in some other species (7, p. 618, Figs. 223, 224).

## 81. CACTACEÆ

Flower ♂, hemicyclic, actinomorphic, rarely becoming zygomorphic later, syngonous. Perianth and andrœcium acyclic. Perianth members (tepals) generally  $\infty$  seldom 10 or fewer, intergrading from sepals to petals, some or all conjoined into a tube. Stamens  $\infty$ , generally springing from the perianth tube, rarely direct from the axis. Carpels 2-10 ( $-\infty$ ) in one series, all consolidated and fertile. Ovary often more or less sunk in the axis, unilocular, the placentæ rarely projecting far into the cavity. Style single, varying in thickness with variations in the number of carpels, sometimes hollow. Stigma lobes as many as the carpels and standing over the carpels. Ovules generally numerous, less often few on each placenta. Fruit a berry.

The vascular ground-plan shows no definite pattern, consequently the whole system is difficult to analyse. In general, the bundles for the outermost tepals turn outwards in the ordinary way on the corresponding radii. The residual bundles of the cylinder break up irregularly, giving rise centripetally to those serving the inner series. The carpels are without separate midrib bundles. The placental bundles form branches which extend laterally since  $> 2$  rows of ovules are borne on each placenta and also downwards so that at the base of the loculus these branches appear in transverse section to be unconnected with the main vascular system. Above the ovule level a single bundle is prolonged from each placenta into the style, one such bundle passing into each stigma. Hence the number of these bundles in the style and the number of stigma lobes afford the readiest clue to the number of carpels present.

A similar apparent lack of connection at the base of the loculus between the placental and the main vascular system is noticeable in the syngonous flower of *Punica* (see under Punicaceæ later in the present Volume, Part 8, p. 279).

## ILLUSTRATIVE TYPES

**Rhipsalis** spp. (e.g. *R. Cassytha*). Tepals 10 or

fewer G 2-4. Ovary not sunk in the tissue of the axis. Ovules in few series on each placenta.

**Opuntia spp.** Tepals  $> 10$ . G 2-10. Ovary sunk in the tissue of the axis. Ovules in many series on each placenta.

## 82. THYMELÆACEÆ

Flowers generally ♂, rarely polygamous or dioecious (occasionally in *Pimelea*, constantly in *Daphnopsis*), often di- or trimorphic, almost always actinomorphic and hypogynous, with an isomerous 4- or 5- rarely 6-merous perianth and andrœcium, but usually with an oligomerous gynœceum. Perianth tubular, petaloid, often persistent, sometimes 1-seriate, sometimes consisting of calyx and corolla. Tepals in the former case, and sepals in the latter, with commissural marginal veins, both tepals and sepals being coloured (see below). Andrœcium of two whorls isomerous with the perianth whorls, or the outer whorl suppressed; only in *Pimelea* reduced to two antepalous members. Filaments conjoined with the perianth tube, becoming free at various levels, the outer whorl usually at a higher, the inner at a lower level. Gynœceum generally unilocular of 2-8 carpels of which only one is fertile; rarely bilocular and of 4 carpels, 2 sterile, 2 fertile (*e.g.* *Peddiea*). Ovary sessile or borne on a longer or shorter stipe, often surrounded at the base by a cup-shaped outgrowth of the axis. Style single, long or short, springing from the top of the ovary or from the posterior face, derived (? always) from sterile and fertile carpels. Stigma capitate, club-shaped, punctiform or cylindrical. Ovules solitary in the loculus, pendulous from near the top of the ovary. Fruit nut-like, drupaceous or capsuloid, sometimes enclosed in the fleshy base of the perianth tube.

The Thymelæaceæ afford examples, also seen in *Thomasia* (see under Sterculiaceæ in Vol. I, Part 4, p. 118; also 19b, p. 204, Fig. 9) of the exceptional condition in which the petals still retain distinct morphological form in some degree after the vascular system has been lost, the whole of the trunk cords on the petal radii in Thymelæaceæ being used up in supplying the marginal venation systems of



the petaloid sepals and the antepetalous stamen bundles (e.g. *Gnidia spp.*). The median splitting of the non-vascular petals in some species (e.g. *Gnidia carinata*) into twin halves corresponds with the bifurcation at the same level of the trunk cords on these radii although no portion of these cords now enters the reduced petal structures. Since in *Gnidia spp.* having non-vascular petals commissural marginal veins are present in the sepals comparable with those present in the tepals of the genera which lack a corolla, these sepals like the tepals are coloured (see Vol. I, Introduction, pp. 9, 10; and for other examples of the coloration of tepals in the latter circumstances see earlier in the present Volume under Cephalotaceæ, Part 5, p. 142, Saxifragaceæ (*Chrysosplenium*), Part 5, p. 156, Polygalaceæ, Part 6, p. 205, Flacourtiaceæ, Part 7, p. 253), and later in the present Volume under Combretaceæ, Part 8, p. 284).

The vascular bundles of the stamens do not arise independently, but are carried outwards as components of the trunk cords originating on the sepal and the petal radii, respectively. Hence, when the outer staminal whorl is suppressed, the inner whorl retains its antepetalous position as in *Struthiola* (see below under Illustrative Types).

## ILLUSTRATIVE TYPES

### AQUILARIOIDEÆ-AQUILARIEÆ

**Aquilaria spp.** Flower ♀. K 5 (or 6) C 5 (or 6) A 5 (or 6) + 5 (or 6) G 2, sterile + 2, fertile. Petals entire or divided, sometimes to the base. Ovary with short stipe, bilocular. Ovules 2. Style long or short. Stigma large, discoid. Fruit a capsule, surrounded at the base by the persistent perianth-stamen tube, dehiscent loculicidally.

### PHALERIOIDEÆ-PHALERIEÆ

**Phaleria** (19b, p. 208). Flower ♀. K 4 (or 5) ± C 4 (or 5) A 4 (or 5) + 4 (or 5) G 2, sterile + 2, fertile. Petals when present in the form of thick lappets. Ovary almost sessile, bilocular. Ovules 2. Style filiform. Stigma capitate. Fruit drupaceous.

PHALERIOIDEÆ-PEDDIEÆ

**Peddiea Dregei** (19b, p. 208). Flower ♂. Perianth single. T 4 (or 5) A 4 (or 5) + 4 (or 5) G 2, sterile + 2, fertile. Ovary with short stipe, bilocular. Ovules 2. Style short. Stigma capitate. Fruit a drupe enclosed in the persistent perianth-stamen tube.

THYMELÆOIDEÆ-GNIDIEÆ

**Gnidia spp.** (e.g. *G. carinata*, *G. pinifolia*, *G. socotrana*) (19b, p. 208). Flower ♀. K 4 (or 5) C 4 (or 5), entire (*G. pinifolia*) or split to the base (*G. carinata*) or absent (*G. socotrana*), A 4 (or 5) + 4 (or 5) G 1, sterile + 1, fertile. Ovary sessile, unilocular. Style lateral. Stigma capitate. Ovule 1. Fruit nut-like, surrounded by the persistent base of the perianth-stamen tube.

**Struthiola spp.** Flower ♂. K 4 C 4 A 0 + 4 G 1, sterile + 1, fertile. Ovary sessile, unilocular. Style lateral. Fruit as in *Gnidia* (see above).

THYMELÆOIDEÆ-DAPHNEÆ

**\*Daphne Mezereum** (19b, p. 208, also p. 212). Flower ♀. T 4 A 4 + 4 G 8-6 of which only one is fertile. Ovary sessile, unilocular. Ovule 1. Style very short. Stigma large, capitate. Fruit a drupe.

**Lachnæa spp.** Flower ♂, slightly zygomorphic owing to difference of size in the tepals. T 4 A 4 + 4 G 1, sterile + 1, fertile.

THYMELÆOIDEÆ-PIMELEÆ

**Pimelea** (19b, p. 208). Flower ♀, or rarely polygamous or dioecious. T 4 A 2 + 0 G 1, sterile + 1, fertile. Ovary unilocular. Ovule 1. Style lateral. Stigma capitate.

## 83. ELÆAGNACEÆ

Flower ♂, polygamous, or unisexual and diœcious, actinomorphic. Perianth single. Segments generally 2, 4 or 5, rarely more, united in ♂ or ♀ flowers to form a tube enclosing the whole or the lower portion of the ovary, persistent in whole or in part. Stamens in two 4-merous whorls, or 5 or 4 in a single whorl. Carpels 2, median, 1 sterile, 1 fertile. Ovary unilocular. Ovule solitary, basal. Style single, filamentous. Stigma terminal, unilateral or extending round the opening of the stylar canal. Fruit achene-like, with membranous pericarp, enclosed in the persistent perianth, 1-seeded, indehiscent.

## ILLUSTRATIVE TYPES

**\*Hippophæ rhamnoides** (Sea Buckthorn). Flowers unisexual and diœcious. ♂ Flower. Perianth segments 2, each (probably) of 3 tepals (see below) A 4, disposed round a 4-angled disc. ♀ Flower hypogynous. Perianth as in the ♂ flower. G 2, one sterile, one fertile, both forming the wall of the ovary and prolonged into the style and stigma. Style filamentous, channelled on the inner face, the stylar canal opening to the surface along the channel which opens out and becomes stigmatic above the perianth tube. Fruit a spurious berry, the true fruit being enclosed in the persistent perianth which becomes succulent.

The vascular system of the perianth in both sexes consists of six bundles which arise on separate radii and take up equidistant positions, three passing into each segment. This vascular ground-plan indicates a floral ground-plan of six tepals, each of the two perianth segments consisting of three completely fused together.

After the six vascular bundles for the perianth in the ♀ flower have turned outwards at the flower base the residual vascular elements serving the gynœceum are reformed into

a new complete cylinder. Those elements lying in the median plane to the front are organised into the midrib bundle of the sterile carpel. The rest become aggregated in the median plane at the back and 'condensed' into the twin placental bundles of the fertile carpel. Sterile carpel midrib and the placental bundles of the fertile carpel are prolonged up the style and stigma which are thus formed of both carpels. As the loculus makes its appearance the ovary wall becomes cleft between the placental strands so that the loculus communicates with the exterior. This cleft is not resealed as it is in almost all similarly constructed ovaries when exposed (superior). It thus divides the fertile carpel in half, continuing upwards until it widens out in the region of the stigma.

**Lepargyræa (Shepherdia) canadensis.** Flowers unisexual and diœcious. ♂ Flower. T 4 A 4 + 4. ♀ Flower. T 4 G as in *Hippophæ* (see above). Fruit a spurious berry.

**Elæagnus spp.** Flowers ♂ or polygamous. ♀ Flower. T 5 A 5 or T 4 A 4 G as in *Hippophæ* (see above). Fruit a spurious berry. ♂ Flower with a style filament representing a rudimentary gynæceum.



## Part 8

### Dicotyledons

Family	84.	Lythraceæ
„	85.	Punicaceæ
„	86.	Lecythidaceæ
„	87.	Rhizophoraceæ
„	88.	Combretaceæ
„	89.	Myrtaceæ
„	90.	Melastomataceæ
„	91.	Hydrocaryaceæ
„	92.	Ænotheraceæ (Onagraceæ)
„	93.	Haloragaceæ
„	94.	Hippuridaceæ
„	95.	Thelygonaceæ
„	96.	Araliaceæ
„	97.	Umbelliferæ
„	98.	Cornaceæ
„	99.	Garryaceæ



## 84. LYTHRACEÆ

Flower ♂, actinomorphic or rarely zygomorphic, hypogynous; in its fullest development six-whorled and isomerous throughout ( $K\ n\ C\ n\ A\ n + n\ G\ n$ , sterile +  $n$ , fertile), but generally with reduction in the gynæceum; sometimes with suppression of the corolla, or wholly or in part, of the antesepalous stamen whorl or of the antepetalous stamen whorl; sometimes with multiplication by branching of the antepetalous stamen whorl or of both stamen whorls; usually 4- or 6-merous but varying from 3- to 16-merous; with a longer or shorter calyx-corolla-andrœcium flower wall often furnished with teeth or wings alternating with the sepals. Petals generally becoming free at the top of the flower wall, the stamens at a lower level. Gynæceum syncarpous. Sterile carpels and loculi when isomerous antesepalous in some six-whorled types (*Lagerstrœmia*, 28†), antepetalous in others (*Ammannia coccinea*, *A. octandra*). Ovary multilocular, becoming unilocular at the summit as the fertile carpels separate at their inner face to give rise to the stylar canal, rarely unilocular throughout. Ovules generally  $\infty$ , in numerous rows on each placenta. Style single. Stigma terminal, punctiform or slightly bilobed. Fruit a capsule, dehiscing variously or sometimes remaining closed.

The midrib bundles for each member of the perianth and of the andrœcium lying on any one radius are derived from the single trunk cord on that radius or from the same delimited vascular unit of the central cylinder. In these circumstances the antepetalous position of the sterile carpels and loculi in some six-whorled tetramerous types (e.g. some *Ammannia* spp., see above) is probably attributable to the fact that in such types the sepals occupy the flat sides, and the petals the angles of the four-sided ground-plan and that the outer carpels develop where there is most room, i.e. on the longer radii, the radii of the angles (see also earlier in the present Volume under *Rhodotypos* (Rosaceæ), Part 5, p. 174). Both sterile



and fertile carpels with midrib bundles or fertile carpels without these bundles.

### ILLUSTRATIVE TYPES

**Lagerstroemia indica** (28, pp. 301-304, with Figs. 6 and 7). Flower actinomorphic, hexamerous throughout, with multiplication through branching of the antepetalous stamen whorl. Ovary becoming unilocular above as the loculi open into the basal region of the stylar canal. Fertile carpels without midrib bundles. Sterile carpel midribs and placental bundles of the fertile carpels prolonged into the style. Loculi antesepalous. Fruit a capsule, dehiscing loculicidally through median radial splitting of the sterile carpels.

**Lagerstroemia Flos-reginæ** (28, *loc. cit.*). Flower with multiplication through branching of both staminal whorls, otherwise similar to *L. indica* (see above).

In this genus, as the several loculi come into being, the sterile carpels never completely withdraw into the ovary wall but project into the loculi as longitudinal ribs. The same condition occurs in more pronounced form in *Linum* (see under Linaceæ in Vol. I, Part 3, pp. 76, 77; also 3, pp. 150, 151, and p. 148, Figs. 55-58).

**\*Lythrum Salicaria** (Purple Loosestrife). Flowers trimorphic, actinomorphic, hexamerous in the perianth and andrœcium with a dimerous gynœceum (K 6 C 6 A 6 + 6 G 2, sterile + 2, fertile). Sepals with outgrowths between them. Ovary bilocular. Fertile as well as sterile carpels with midrib bundles. Fruit a capsule, dehiscing septicidally through median radial splitting of the fertile carpels.

An unusual feature in the vascular system of the flower wall is the formation of a complete vascular girdle immediately below the level at which the sepals and petals become free through the development from the sepal midribs of a pair of horizontal lateral branches which anastomose with the neighbouring petal midrib on each side. From each of these nodal

points on the petal radii another bundle originates which passes into the outgrowth between the sepals lying on the corresponding radius. This bundle represents the completely fused adjacent commissural laterals of the sepal on either side. This interpretation receives support from the fact that in *Peplis Portula* two bundles arise from each of these nodal points, but instead of entering the calyx outgrowth on the corresponding radius, they diverge and become a commissural marginal vein of the sepal on either side (see below). The formation of similar paired appendages on the sepals occurs also in species of *Nemophila* among Hydrophyllaceæ, where, owing to the absence of anastomosis, the vascular relations are diagrammatically simple (see under this Family later in the present Volume, Part 12, p. 441).

**\*Peplis Portula** (Water Purslane). Perianth and andrœcium hexamerous. Corolla sometimes, antepetalous stamens usually, suppressed. Gynœceum dimersous. (K 6 C 6 or 0 A 6 + 0 G 2, sterile + 2, fertile.) Calyx generally with non-vascular teeth alternating with the sepals. Sepals with commissural marginal veins. Ovary bilocular. Fertile as well as sterile carpels with midrib bundles, both pairs of bundles being prolonged into the short style. Fruit indehiscent.

**Cuphea ignea** (3, pp. 151-153 with Figs. 60-63). Flower zygomorphic. K 6, the posterior member spurred C 0 A 5 + 6 G 2, sterile + 2, fertile. Below the ovary a dorsal disc. Ovary bilocular. Sterile carpels with midrib bundles which are prolonged into the style. Fertile carpels without midrib bundles. After fertilisation the central column formed of the two conjoined placentæ elongates, ruptures the ovary wall and protruding through the opening and the split calyx bends backwards.

The perianth and andrœcium are supplied by twelve vascular cords, those on the sepal radii furnish the sepal midribs and antesepalous stamen bundles, those on the petal radii the petal midribs in species in which members of the corolla are present and the antepetalous stamen bundles. It follows that the suppression of some, or of all of the petals, as in *C. ignea*, will not affect the radial position of the succeeding whorls.

**Lawsonia.** K 4 C 4 A 4<sub>1</sub> + 0 G 2 sterile + 2, fertile. The eight stamens stand in pairs in front of, but at some distance from, the mid-line of each sepal.

The vascular bundles for the stamens, all of which belong to the antesepalous whorl, are not detached directly from the trunk cords on the sepal radii, as in other genera in the Family, but from the primary pair of lateral branches formed by the sepal midribs, hence the duplication of this whorl of the andrœcium and the shifting of the individual stamens away from the mid-line of the sepals. Duplication of the members of a staminal whorl associated with the derivation of their vascular bundles (when not of independent origin) from the primary pair of laterals of the corresponding trunk cord instead of directly from the trunk cord itself is of fairly common occurrence. But it is met with far more frequently in the antepetalous than in the antesepalous whorl (see *e.g.* earlier in the present Volume under Rosaceæ and Hamamelidaceæ, Part 5, pp. 177 and 164, respectively ; and later in the present Volume under Styracaceæ and Cucurbitaceæ, Part 11, p. 422, and Part 14, p. 489, respectively). For other instances of similar duplication in the antesepalous whorl, see those cited earlier in the present Volume under Tremandraceæ, Part 6, p. 202, and later in the present Volume under Butomaceæ and Hydrocharitaceæ, Part 15, pp. 540 and 543, respectively.

## 85. PUNICACEÆ

Flower ♂, actinomorphic, more or less syngonous. K 5-8, valvate, persistent C 5-8 A  $\infty$ , arranged in successive rings but without apparent relation to the perianth radii G consisting of one, two or three tiers of carpels, the numbers in each tier decreasing successively; each tier of two alternate whorls forming a single ring, the one whorl sterile, the other fertile. Ovules  $\infty$ , in numerous rows on each placenta. Style single. Stigma terminal, slightly lobed with lobes equal in number to the fertile carpels in the outermost (oldest) tier and centred over these carpels ('commissural'). Fruit a berry.

The unusual arrangement of the carpels in separate tiers comes about as the result of the large number developed and the limited area of axis surface available at one time. As the first tier develops 5-10 loculi, separated by a corresponding number of thin partitions, appear round a central core of axial tissue. The partitions represent as many sterile carpels. On the alternate radii projecting into each loculus from its inner face is a placental bulge covered with ovules and having a central vascular bundle. Each bulge corresponds with a consolidated fertile carpel. As growth proceeds the fertile carpels extend outwards horizontally and then curve upwards so that each corresponding placental bulge, which originally projected outwards into the loculus from the central axial core, now forms the outer boundary of the loculus and projects inwards. Thus arises a unique type of ground-plan in which it is those carpels external to, and on the radius of, each loculus which are fertile, and the alternate carpels forming the septa which are sterile.

The effect of the above development away from the centre is to permit of a repetition nearer the centre of this whole series of processes, a second tier of a smaller number

of alternate sterile and fertile carpels being formed around the now smaller central axial core in the same way as the outer tier; and sometimes even a third tier within the second. The larger the number of carpels which succeed in developing in the first (outer) tier the fewer in the second tier; the smaller the number in the outer tier the greater the likelihood of the development of a third tier. If the same number develop in the first and second tiers the carpels of the one kind in the second tier alternate with those of the same kind in the first. In each tier the fertile carpels at their extreme base lie on the axial side of the developing loculi, each forming the inner boundary of the corresponding loculus with its placenta projecting outwards into the cavity. As the carpel curves outwards and then upwards it comes to form the floor and then the outer boundary of the loculus with its placenta now projecting inwards into the cavity. It follows that the mode of placentation is not 'axile' in the innermost and 'parietal' in the older outer tier(s), as must be supposed did the fertile carpels merely represent the fertile margins of the carpels forming the septa, but is identical for the ovule-bearing carpels of all the tiers, these carpels being distinct from those forming the septa which are sterile.

As the carpels of the outer tier become disjoined at the summit of the ovary from the perianth-androecium wall they curve inwards, roofing-in the loculi and then, turning upwards again, form the hollow style. Only the fertile carpel vascular bundles enter and pass up the style to the stigma level, the number of stigmatic lobes corresponding with the number of these fertile carpels, each lobe standing over one of these bundles. The carpels of the second and third tiers take no part in the formation of the style, being entirely enclosed within the outer tier. The loculi of these inner carpels open into a central cavity continuous above with the stylar canal.

The vascular system of the gynæceum appears to arise free in the central ground tissue below the ovary as a meshwork, being unconnected at this level with the main vascular cylinder. From this meshwork are differentiated (1) a ring of weak bundles, each of which turns outwards along a septum representing a consolidated sterile carpel of which this bundle is the midrib; and (2) an alternate ring of stronger bundles which bear the ovules and represent the midrib bundles of a corresponding number of consolidated fertile carpels. A residuum of the central meshwork furnishes in the same way the bundles for the succeeding tier(s).

The serial development of the carpels, rendered inevitable by their large number and the limited area of axis surface available at any one time for their accommodation, finds a certain parallel in the section Malopeæ among Malvaceæ and in *Nolana atriplicifolia* (Nolanaceæ) (see under these Families in Vol. I, Part 4, p. 108, and in the present Volume, Part 12, p. 451, respectively), with this difference, that in both Malvaceæ and Nolanaceæ development proceeds uninterruptedly and results in *Nolana atriplicifolia* in an irregular arrangement and in Malopeæ in vertical grouping in 'fields' of separate ovaries consisting (through pseudo-apocarpy) of  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels. While in Punicaceæ development is rhythmic and the resulting tiers of carpels remain united into a single syncarpous gynæceum.

### ILLUSTRATIVE TYPES

**Punica granatum** (Pomegranate). See the characters of the Family.

## 86. LECYTHIDACEÆ

Flower ♂, actinomorphic or with a zygomorphic corolla and andrœcium, syngonous or perigynous. K (generally) 4-6 C 4-6, sometimes wanting A  $\infty$  in several rings, some often antherless. Filaments joined from the base upwards for a longer or shorter distance. Beneath the andrœcium a ring of glandular tissue. G 2-6 (or more), sterile + 2-6 (or more), fertile. Ovary with 2-6 (or more) loculi. Ovules 1- $\infty$  in each loculus. Style single. Stigma club-shaped, discoid or capitate, with lobes or lappets or entire. Corolla and andrœcium borne on a flat disc; an intra-staminal ring-shaped disc also usually present. Fruit drupaceous or berry-like or a capsule, often opening by a lid.

## ILLUSTRATIVE TYPES

**Napoleona spp.** Flower perigynous, actinomorphic. K 5, valvate C 0 A  $\infty$ , free G 5, sterile + 5, fertile. Ovary with 5 loculi below, becoming unilocular above as the central parenchyma of the axis comes to an end and the fertile carpels become free on their inner face. Ovules solitary in the loculi. Style thick, ending in a 5-angled plate. Stigmas 5, radiating from the centre of the plate to the angles along the lines of the 5-rayed opening of the stylar canal. Fruit baccate.

Sterile carpels with midrib bundles which are prolonged into the style. Fertile carpels with placental, but without separate midrib bundles in the region of the ovary. As the ovary passes into the style, strands from the peripheral vascular ring supplying the andrœcium turn inwards on the fertile carpel radii. These strands, representing fertile carpel midribs which only become separate at this level, are continued up into the style which thus represents all ten carpels, hence its thickness.

**Bertholletia excelsa** (Brazil-nut). Flower syngonous, zygomorphic. K 6, united into two 3-toothed segments, C 6 A monadelphous below, free above, bent to one side in the form of a helmet G 4, sterile + 4, fertile. Ovary quadrilocular. Ovules in 2 rows in each loculus. Style long, tapering. Stigma very small, terminal. Fruit with fleshy epicarp and hard endocarp opening by a very small lid corresponding with the top of the placental column. As the fruit matures it becomes unilocular, the fertile carpels (septa) tearing across and disappearing, leaving the inner ends still soldered together as a 4-angled central column tapering upwards, the angles corresponding with the torn surfaces. [The thickened lower end of this broken column is often to be found mixed with the nuts in commercial material.]



## 87. RHIZOPHORACEÆ

Flowers ♂, or rarely through abortion polygamous, actinomorphic, more or less syngonous. K 4-8 (or more) C 4-8 (or more) A 4-8 + 4-8 or  $\infty$  G 2-4, sterile + 2-4 fertile. Within the andræcium a single or double lappeted disc. Ovary with as many loculi as fertile carpels, sometimes becoming unilocular above as these carpels no longer fuse in the centre, rarely unilocular throughout. Styles generally connate, rarely separate (3 or 4) and centred over the sterile carpels. Stigmas, when distinct, as many as the sterile carpels and centred over these carpels, terminal. Ovules generally 2 in each loculus, rarely more or solitary. Fruit generally baccate, seldom drupaceous, or a capsule dehiscing eventually loculicidally, or indehiscent.

### ILLUSTRATIVE TYPES

**Rhizophora Mangle** (Mangrove). Flower partially syngonous. K 4 orthogonal, C 4 diagonal, A 4 + 4 diplostemonous, G 4 orthogonal, 2 sterile, 2 fertile. Style single. Stigma lobes 2, not enlarged, erect. Ovules 2 in each loculus. Fruit baccate.

Sepals with commissural marginal veins. Antesepalous and antepetalous stamen bundles conjoined at first with the sepal and petal midrib bundles, respectively. As the detached antesepalous staminal bundles stand slightly further from the centre than the corresponding antepetalous bundles the arrangement is primarily diplostemonous.

## 88. COMBRETACEÆ

Flowers generally almost sessile, sometimes becoming raised in the fruiting stage through development of the pedicel, ♀ or sometimes unisexual through abortion, actinomorphic or very slightly zygomorphic, syngonous. Perianth of calyx and corolla or reduced to one whorl. Andrœcium of two whorls or one-whorled through suppression of the antepetalous whorl. The whorls of the perianth and andrœcium isomerous, either pentamerous or tetramerous, united for a longer or shorter distance forming the flower wall. Lining the flower wall at the bottom a ring of glandular tissue, sometimes lappeted. Gynœceum (generally) of 2 sterile and 2 fertile carpels. Ovary unilocular. Style single. Stigma generally punctiform, rarely capitate. Ovules few, pendulous from the upper part of the wall of the loculus. Fruit dry, often angled or winged, indehiscent or incompletely dehiscent, one-seeded.

The vascular scheme of the flower wall exhibits a very unusual feature. A single set of trunk cords on one set of radii furnishes the midrib bundles for the perianth and andrœcium members on this set of radii, and also those for the perianth and andrœcium members on the alternate set of radii when these are present. These cords, five in pentamerous types, run up the flower wall in line with the sepals. After the antesepalous stamen bundle has been detached a residual portion of each cord continues upwards to become a sepal midrib. Immediately below the level at which the sepal segments become free a horizontal lateral branch is given off on each side by all five trunk cords. The lowest set of these horizontal branches meet midway between the cords, and from each of the five points of junction a bundle originates which enters the antepetalous stamen. In types with a corolla the same development is repeated at a slightly higher level. New points of junction, standing in line with those formed at the lower level again result from the meeting of this higher set of lateral branches, and from these points the petal midrib bundles take their rise. Further true lateral

branching occurs in the free sepal segments, but there are no marginal veins of commissural origin.

In types in which the perianth consists of a single whorl the vascular scheme differs from that described above in that from the junction points formed at the higher level there is no development of a petal midrib bundle, but a horizontal lateral branch on each side becomes a marginal vein of the neighbouring tepal on each side, anastomosing in its course with the true lateral veins arising from the midrib of the tepal. Hence the tepals of such types are coloured (*i.e.* non-green) along the margins or over the whole surface (see Vol. I, Introduction, pp. 9, 10, and under *Thomasia* among Sterculiaceæ, Part 4, p. 118; also in the present Volume under Cephalotaceæ and *Chrysosplenium* (Saxifragaceæ), Part 5, pp. 142 and 156, respectively; Polygalaceæ, Part 6, p. 205, and Thymelæaceæ, Part 7, p. 266; also 19a and 19b).

A similar girdle of fibro-vascular strands is formed at the top of the flower wall in the allied Families Lythraceæ and Melastomataceæ, but in these latter Families this feature is not associated with the peculiar method of formation of the petal midrib and antepetalous stamen bundles characteristic of Combretaceæ (see earlier in the present Volume, Part 8, p. 274, and later, Part 8, p. 288, respectively). On the other hand, in the unrelated Family Cistaceæ with hypogynous flowers, the petal midrib bundles originate as in Combretaceæ from the points of junction of horizontal lateral branches derived from antesepalous cords. But in Cistaceæ this process is not duplicated in the formation of the vascular bundles of the andrœcium, since an antepetalous stamen whorl is lacking (see earlier in the present Volume under Cistaceæ, Part 7, p. 250; also 26, p. 50, Fig. 3, and p. 58, Fig. 18).

The vascular bundles of the fertile carpels are organised at the flower base from residual elements detached from the inner face of the primary trunk cords. Those of the sterile carpels are organised in the same way but only become detached at a higher level. As the loculi close, the fertile carpel bundles divide in half. The resulting twin strands diverge and coalesce, respectively, with the neighbouring sterile carpel midrib on each side. Hence only two separate bundles enter the single style, each bundle representing the vascular systems of  $\frac{1}{2}$   $\times$   $\frac{1}{2}$  carpels.

## ILLUSTRATIVE TYPES

**Combretum spp.** (*e.g.* *C. platypetalum*, *C. nanum*).

K 4 C 4 A 4 + 4 G 4, 2 sterile, 2 fertile. Sepals without

marginal veins of commissural origin. Stigma undivided. Fruit dry, often 5-angled or with 5 wings.

**Terminalia Catappa.** Flowers ♀ and ♂, almost sessile. ♀ Flower. T 5 with marginal veins of commissural origin, coloured (*i.e.* non-green) A 5 + 5 G 4, 2 sterile, 2 fertile. Stigma punctiform. Fruit slightly angled, stalked. ♂ Flower similar but lacking both sets of carpels and all carpellary vascular bundles.

## 89. MYRTACEÆ

Flowers almost always ♂, actinomorphic, more or less syngonous. K 4 or 5, persistent, sometimes reduced to teeth or wanting (*Eucalyptus*). C 4 or 5, seldom fewer or wanting. A generally  $\infty$  and arranged regularly in successive rings but without definite relation to the perianth radii, sometimes united in bundles which are then usually antepetalous (as *e.g.* in *Calothamnus*, *Melaleuca*, *Beaufortia*), seldom limited in number and in distinct whorls ( $5 + 0$  or  $5 + 5$  or  $5 + 5_x$ ); when in two whorls obdiplostemonous. Filaments free. Beneath the androecium generally a ring of glandular tissue. G 2-5 (or more), sterile + 2-5 (or more), fertile; or sometimes when reduced to  $2 + 2$  only one carpel of the inner whorl actually, the other merely potentially fertile. Ovary with 2-5 (or more) loculi when the fertile carpels extend to the centre, unilocular when they fail to do so.

The exceptional development of the sterile carpels in some genera (*e.g.* *Rhodomyrtus*) in which these carpels project so far into each loculus between the two rows of ovules as to divide it almost completely in two, gives rise to the deceptive appearance that the number of loculi is twice that of the carpels in one whorl. This feature occurs in a less pronounced form in *Lagerstrœmia spp.* (see under Lythraceæ earlier in the present Volume, Part 8, p. 274) and in a more extreme degree in *Linum*, in which both sterile and fertile carpels give rise to complete septa in the lower region of the ovary so that in this region the number of loculi is in reality twice that of the carpels in one whorl (see under Linaceæ in Vol. I, Part 3, p. 76).

Ovules in 2-several rows on each placenta. Style single. Stigma terminal, generally small and entire, rarely enlarged with a polygonal outline. Fruit a berry, drupe or capsule, or nut-like and indehiscent, few- or 1-seeded.

Among genera included in the Family are *Myrtus*

(Myrtle), *Eucalyptus*, *Eugenia Pimenta* (Allspice), *Jambosa Caryophyllus* (Clove), *Psidium spp.* (Guava).

### ILLUSTRATIVE TYPES

**Myrtus** (Myrtle). K 4 C 4 A  $\infty$  in rings, G 2 (or 3), sterile + 2 (or 3), fertile. Sepals cohering in the bud. Ovary bi- (or tri-) locular below, becoming unilocular above as the fertile carpels fail to reach the centre. Ovules in several rows on each placenta. Stigma small, simple. Fruit a berry.

The central vascular cylinder enlarges at the flower base and at the same time breaks up into a large number of bundles distributed on many radii and extending various distances from the centre. Each of the four sepals receives several of these bundles in place of a single midrib. These several features obscure the relation of the numerous staminal bundles to the perianth sectors. Strands detached from some of the innermost bundles shortly turn inwards and become organised into the placental strands of the two fertile carpels. At a higher level the sterile carpel midribs are detached from the inner face of two opposite bundles in the lateral plane. But only as the loculi close are strands detached from bundles in the median plane to become the corresponding bundles of the fertile carpels. Both sterile and fertile carpel bundles enter the single style, which in a G 2 + 2 flower thus receives four bundles.

**Leptospermum spp.** (e.g. *L. scoparium*, G 6-3, sterile + 6-3, fertile, *L. lævigatum*, G 6-10, sterile + 6-10, fertile). Sepals free, broad. Fruit a capsule, dehiscing loculicidally through median radial splitting of the sterile carpels.

**Eucalyptus.** Sepals reduced to minute teeth or wanting. Petals united into a cap, falling in one piece. Fruit a capsule dehiscing at the summit loculicidally.

## 90. MELASTOMATACEÆ

Flower ♂, generally actinomorphic, six-whorled, isomeric throughout and either pentamerous or tetramerous (K 4 or 5 C 4 or 5 A 4 or 5 + 4 or 5 G 4 or 5, sterile + 4 or 5, fertile), hypogynous or more or less syngonous; when hypogynous or incompletely syngonous with a longer or shorter perianth-andræcium flower tube, sometimes with teeth or outgrowths from the rim of the tube alternating with the sepals as in some Lythraceæ (see under that Family earlier in the present Volume, Part 8, p. 273). Stamens often dimorphic. Ovary almost always multi-locular. Sterile carpels and loculi, with perhaps one exception (*Rhexia*), antesealous (28, p. 305). Ovules generally  $\infty$  in numerous rows in each loculus. Style single. Stigma punctiform, or capitate and then sometimes undivided, sometimes lappeted. Fruit a capsule or capsuloid, with loculicidal dehiscence through median radial splitting of the sterile carpels; or a berry.

The Melastomataceæ afford particularly favourable material for observation of the process which leads to the syngonous condition. For the series of grades occurring within the Family between the fully syngonous and the hypogynous condition provide clear proof that the former state is simply the outcome of the fusion of the outer wall of the ovary with the bases of the sepals, petals and stamens which are themselves fused below into a common compound structure—the wall of the flower tube.

The vascular arrangement in the flower wall shows the same unusual feature as that which characterises the Combretaceæ, a continuous girdle of vascular tissue being formed immediately below the level at which the sepals and petals become free through the junction of horizontal branches derived from the vertical trunk cords. But the two Families differ in that in Combretaceæ the petal midrib bundles arise from the points of junction of such horizontal branches (see

earlier in the present Volume under Combretaceæ, Part 8, p. 283), as also is the case in Cistaceæ (see earlier in the present Volume, Part 7, p. 251), whereas in Melastomataceæ, trunk cords originate on the petal as well as on the sepal radii at the flower base, and furnish the petal midribs and antepetalous stamen bundles. The presence of the full number of trunk cords in this Family is readily observed in the thin flower wall of *Centradenia floribunda* when this structure, after being rendered transparent, is split open and viewed flat.

### ILLUSTRATIVE TYPES

***Centradenia floribunda*** (28, p. 305 and p. 302, Fig. 5). Flower tetramerous (K 4 C 4 A 4 + 4 G 4, sterile + 4, fertile), syngonous below but the ovary completely free towards the top. Flower tube without teeth alternating with the sepals. Stamens of the two whorls of different size. Fruit capsuloid.

A single trunk cord on each radius furnishes the midrib bundles for all the members on that radius. Those on the sepal radii give rise to the sepal midribs, antesepalous stamen bundles and sterile carpel midribs; those on the petal radii simply to the petal midribs and antepetalous stamen bundles, since the fertile carpels lack a separate midrib bundle. The sepals occupy the angles of the 4-sided flower base, consequently the sterile carpel midribs are detached from the cords on the sepal radii since more room is available on these radii than on those of the petals which are exerted from the flat sides. These relations are the opposite of those obtaining in tetramerous types in Enotheraceæ (see under that Family later in the present Volume, Part 8, p. 292).

***Tibouchina* spp.** (section *Diptostegium*). Flower generally pentamerous, hypogynous or with the ovary united to the flower tube on the ten radii alternating with the midribs of the perianth members, but being free on the other set of radii.

***Dissotis plumosa*.** Flower generally tetramerous, otherwise as in *Tibouchina* (see above).



## 91. HYDROCARYACEÆ

Flower ♂, actinomorphic, partially syngonous, tetramerous with reduction in the gynæceum. K 4 orthogonal, persistent C 4, diagonal A 4, orthogonal G 4, 2 lateral sterile, 2 median fertile. Surrounding the ovary as it becomes free from the perianth and andræcium a sinuous disc. Ovary bilocular. Ovules solitary in each loculus. Style single. Stigma capitate, entire. Fruit drupaceous, armed with the horn-like projections formed by the persistent sepals, generally unilocular and one-seeded through obliteration of the second loculus and shrivelling of the corresponding ovule.

The vascular system at the flower base consists of eight trunk cords, four in the orthogonal and four in the diagonal planes. As commonly in syngonous types, the placental bundles of the fertile carpels are the first to originate. They are detached from the two orthogonal cords in the median plane and turn inwards to the centre. These two cords and the two in the lateral plane after receiving a horizontal lateral strand from the diagonal cord on each side become the midribs of the four sepals. The four diagonal cords shortly give rise to a second set of horizontal lateral strands before continuing upwards to become the petal midribs. These laterals extend till they meet in the orthogonal planes. From each of the four junction points thus formed, which lie in line with the sepals, are derived the bundle for the corresponding stamen and two or more strands which take the place of a midrib for the corresponding carpel. These strands in both sterile and fertile carpels are continued up the style, but the placental bundles come to an end at the level of origin of the ovaries.

The formation of the midribs of the petals from the meeting points of horizontal branches from the sepal midribs is a characteristic feature in Cistaceæ and Combretaceæ (see under these Families earlier in the present Volume, Part 7, p. 251, and Part 8, p. 283, respectively), but it is exceptional when primary trunk cords have already been formed on both sepal and petal radii for the stamen bundles to arise in this way.

## ILLUSTRATIVE TYPES

**Trapa natans** (Water Chestnut). See the characters of the Family.

## 92. ÆNOTHERACEÆ (ONAGRACEÆ)

Flower ♂, generally actinomorphic and tetramerous, less often 2-, 3-, 5- or 6-merous, rarely zygomorphic, completely syngonous, six-whorled, isomerous throughout ( $K\ n\ C\ n\ A\ n + n, G\ n$ , sterile  $+ n$ , fertile), and primarily diplostemonous; sometimes five-whorled through suppression of the antepetalous stamen whorl (e.g. *Euchari-dium*) or four-whorled through suppression of the corolla as well as the superposed stamens (*Ludwigia*); sometimes with reduction in the remaining staminal whorl (*Lopezia*). When tetramerous with the sepals in the orthogonal and the petals in the diagonal planes. Ovary multilocular, often becoming unilocular at the summit as the fertile carpels fail to reach the centre (e.g. *Fuchsia*, *Epilobium*). Sterile carpels and loculi antepetalous. Style single. Stigmas usually as many as the sterile carpels, in the form of four arms disposed crosswise (e.g. *Ænothera*, *Gaura*, *Godetia*, species of *Epilobium*); or of four leaf-like expansions similarly arranged (e.g. *Clarkia*); or of four short erect lobes which remaining adpressed form a club-shaped end to the style (e.g. *Epilobium* spp.); or of the four sectors which make up the enlarged head of the style and are merely defined by notches (e.g. *Fuchsia*). The arms or lobes usually standing over the sterile carpels (*Ænothera*, *Gaura*, *Godetia*, *Clarkia*, *Fuchsia*, *Epilobium* spp. with club-shaped style), less often standing over the fertile carpels ('com-missural') (e.g. *Epilobium* spp. with spreading arms). Exceptionally, five or more stigmatic arms may be formed in individual flowers having a normal quadrilocular ovary (e.g. *Ænothera*, *Clarkia*, *Godetia*) (see below). Ovules in 2 or in several rows in each loculus or sometimes solitary. Fruit generally dry, splitting loculicidally and septi-fragally so that the inner portion of the fertile carpels is

left as a seed-bearing column in the centre, rarely nut-like and indehiscent, sometimes baccate (*e.g. Fuchsia*).

Sepals generally with commissural marginal veins. In tetramerous types the sepals occupy the sides of the four-sided ground-plan and the petals the angles. The vascular system at the flower base consists of eight main cords corresponding with the sides and angles. Those on the radii of the sides furnish the sepal midribs, antesealous stamen bundles and the fertile carpel midribs (when present) and placental bundles; those on the angle radii the sepal commissural marginal veins, petal midribs, antepetalous stamen bundles and sterile carpel midribs. That the sterile carpels and hence also the loculi should, in these circumstances, arise as in *Fuchsia*, on the petal radii is probably due, as in some six-whorled tetramerous types in Lythraceæ (see under that Family, earlier in the present Volume, Part 8, p. 273), to the greater amount of space available in line with the angles as compared with the sides. For in tetramerous types among Melastomataceæ, where the sepals are situated at the angles and the petals on the sides of the ground-plan, the sterile carpels and loculi are in accordance with these reverse space relations, antesealous as *e.g.* in *Centradenia* (see under this Family earlier in the present Volume, Part 8, p. 289). The vascular ground-plan of some genera (*e.g. Epilobium, Fuchsia*) also resembles that of certain Melastomataceæ in that a continuous horizontal vascular girdle is formed immediately below the level at which sepals and petals become free through the formation of a set of horizontal anastomosing lateral branches derived from the primary trunk cords (see under Melastomataceæ, *loc. cit.*). The junction points of such lateral branches sometimes serve as the points of origin of the bundles serving other structures (see earlier in the present Volume under Lythraceæ, Part 8, p. 274, Combretaceæ, Part 8, p. 283, and Cistaceæ, Part 7, p. 251).

When the loculi and sterile carpels are not found in line with the angles of the outline, their position is sometimes due to secondary causes, as in species of *Epilobium*, in which, as the exertion level is approached, the sepal sectors come to bulge outwards so that radii which at the flower base coincided with the angles at a higher level come to form the flat sides. In other genera, where the loculi and sterile carpels are from the outset situated in line with the flat sides as, *e.g.* in *Oenothera*, the cause appears to be that the midrib bundles of the sterile carpels are only detached from the antepetalous trunk cords at about the level at which the loculi close, whereas

the midrib bundles of the fertile carpels are detached from the antesepalous trunk cords at the base of the ovary. Hence the sepal-stamen component of these cords, in order to accommodate these midrib bundles, of necessity moves further outwards than the still undissociated trunk cords on the alternate radii, thus causing the corresponding radii to project and form the angles of the outline.

Ordinarily, only the four sterile carpel midrib bundles are prolonged into the style, one midrib bundle passing into each of the four stigmatic arms or lobes which then stand over the sterile carpels (e.g. *Cenothera*, *Gaura*, *Godetia*, *Clarkia* and those *Epilobium* spp. having a club-ended style). But exceptionally the break-up of a trunk cord at the level at which the perianth-stamen component becomes free may cause the remaining (carpel midrib) portion to become split in two with the result that  $> 4$  bundles pass into the style which then ends in  $> 4$  stigmatic lobes. Or again, where fertile as well as sterile carpel midribs are present, some of the former bundles may exceptionally be continued into the style with a similar result, the additional lobes then standing over the fertile carpels (e.g. *Clarkia*). Species of *Epilobium* with spreading stigmatic arms differ from the preceding genera in that the arms are 'commissural.' This difference in position is associated with a different vascular scheme. For shortly below the stigma level the four sterile carpel midrib bundles which entered the style divide in two. The twin bundles of each pair thus formed diverge, one member of each pair passing into the stigmatic arm on the one side, the other into the neighbouring arm on the other side. Hence each arm, which thus receives two bundles and is centred on a fertile carpel radius, is formed from the adjacent halves of two neighbouring sterile carpels which have met over, or fused with, the intervening non-vascular fertile member, a construction the opposite of that occurring in the other genera cited above, in which each stigmatic arm is centred on a sterile carpel radius, and is formed from one whole sterile carpel bordered (presumably) by half the adjacent non-vascular fertile carpel on each side.

Since the vascular bundles for the staminal whorls do not arise independently, suppression of the antepetalous whorl, as in *Eucharidium*, does not affect the radial position of the succeeding carpel whorl. Since, furthermore, these bundles are still undetached from the trunk cords of which they are components at the level at which the ovary comes to an end obdiplostemony, when it occurs, is not of primary origin (as it is in those hypogynous types with antepetalous loculi in which the staminal bundles turn out from the central cylinder

independently), but is due to secondary causes, such as differences in level at which the filaments of the two whorls become free or in the position taken up by the filaments after they have become free.

### ILLUSTRATIVE TYPES

**\*Epilobium** (Willow Herb).  $K\ 4\ C\ 4\ A\ 4 + 4\ G\ 4$ , sterile, antepetalous + 4, fertile, antesepalous. Stigma arms 4, long, spreading crosswise ('commissural') as in *E. parviflorum*, *E. hirsutum*; or short, erect, centred over the sterile carpels and adpressed so that the style is club-ended as in *E. tetragonum*. When the arms remain in contact the epidermal cells on the dorsal as well as those on the ventral surface develop papillæ on which the pollen tetrads are able to germinate. Fruit splitting loculicidally and septifragally so that the ripe fruit wall falls away in four pieces, leaving behind the central column formed of the four placentæ.

Fertile carpels without separate midrib bundles. Sterile carpels with midrib bundles detached from the corresponding trunk cords at the base of the ovary. Stigma arms, when spreading, with two vascular bundles representing half the vascular systems of two neighbouring sterile carpels ( $\frac{1}{2}\ \frac{1}{2}$ ); when erect and adpressed, with one vascular bundle representing the whole system of one sterile carpel.

**\*Oenothera** (Evening Primrose). Floral ground-plan as in *Epilobium* (see above). Stigma arms 4, spreading crosswise, standing over the sterile carpels.

Fertile carpels with midrib bundles which are detached from the corresponding trunk cords near the base of the ovary. Sterile carpels with midrib bundles which, unlike those of *Epilobium*, do not become detached from the corresponding trunk cords until the loculi are about to close (see above). Stigma arms with one vascular bundle representing the vascular system of a single sterile carpel.

**\*Ludwigia (Isnardia) palustris**.  $K\ 4\ C\ 4$  minute, non-vascular, or absent  $A\ 4 + 0\ G\ 4$ , sterile, antepetalous + 4, fertile, antesepalous. Ovules in numerous rows on the placentæ. Sepals, and tepals in those forms lacking a corolla,

with commissural marginal veins. The relation between this form of venation and the colour of the tepals is obscured by the occurrence of some amount of reddish colouring in all parts of the plant. In other types, as *e.g.* in *Thomasia* (Sterculiaceæ) (see under that Family in Vol. I, Part 4, p. 118, and 19b, p. 204, Fig. 9), where the structural relations are similar and colouring occurs in the tepals, the coloration is localised and this difficulty does not occur.

**\**Circæa lutetiana*** (Enchanter's Nightshade). K 2, lateral C 2, median A 2 lateral + 0 G 2, median, sterile + 2, lateral, fertile. Ovary bilocular. Ovules solitary in the loculi. Stigma bilobed, the lobes standing over the sterile carpels. Fruit nut-like, two- or one-seeded, indehiscent.

The calyx-corolla-andrœcium flower wall forms a very narrow tube surmounting the ovary and enclosing the style base with which it is conrescent. Lining the mouth of the tube immediately below the level at which the sepal and petal segments become free is a ring-shaped disc surrounding the now free style.

## 93. HALORAGACEÆ

Flowers inconspicuous, sometimes solitary in the axils of the leaves, sometimes in simple or compound inflorescences, ♂ or unisexual and monœcious and then often polygamous, syngonous, usually isomerous throughout, with tetramerous, or less often tri- or dimerous, whorls. When isomerous and six-whorled obdiplostemonous with antepetalous sterile carpels and loculi. Loculi and styles as many as the sterile carpels, the styles standing over these carpels. Ovules solitary in the loculi. Fruit nut-like or drupaceous.

## ILLUSTRATIVE TYPES

**Haloragis spp.** (*e.g.* *H. alata*). Flower ♂, generally tetramerous and six-whorled (K 4 C 4 A 4 + 4 G 4, sterile + 4, fertile), obdiplostemonous. Ovary quadrilocular with antepetalous loculi. Styles 4, centred over the loculi. Stigmas entire. Ovules 4, solitary in each loculus. Fruit indehiscent.

The vascular system for the four outer whorls consists, as ordinarily in tetramerous syngonous types, of eight trunk cords, four in the orthogonal planes which furnish the midribs of the sepals (which occupy the flat sides of the four-sided ground-plan) and the antesepalous stamen bundles; four in the diagonal planes which similarly break up into the midribs of the petals (which stand at the angles) and the antepetalous stamen bundles. The placental bundles of the fertile carpels are organised at the flower base from the residual vascular elements, but neither these carpels nor the sterile members develop midrib bundles. The development of the sterile carpels and loculi on the petal radii is attributable to the same cause as in isomerous, six-whorled, tetramerous *Cenotheraceæ* (see under that Family earlier in the present Volume, Part 8, p. 292), and is naturally accompanied by obdiplostemony, a condition emphasised in *Haloragis* by the turning inwards of the antesepalous stamen bundles as they become detached from the corresponding trunk cords. The four

placental bundles sooner or later divide in half. The resulting twin bundles of each fertile carpel diverge and pass, respectively, into the adjacent style to right and left. Hence each style corresponds to  $\frac{1}{2}$   $\times$   $\frac{1}{2}$  carpels (since the persistence of the intervening sterile member, despite the loss of its vascular system, is indicated by the entire outline of the stigma).

**\*Myriophyllum spp.** (e.g. **\*M. verticillatum**, **\*M. spicatum** (Water Milfoil). The subtending bract with midrib bundle, the two bracteoles non-vascular. Flowers unisexual or polygamous, monœcious, the upper ♂, the lower ♀, tetramerous, often showing suppression of a perianth or a stamen whorl (K 4 C 4 or sometimes o A 4 + 4 or 4 + o G 4, sterile + 4, fertile). Ovary syncarpous, quadrilocular, with antepetalous loculi, becoming pseudo-apocarpous in the fruiting stage. Styles 4, with long slender stigmas, centred over the sterile carpels. Ovules 4, solitary in each loculus. Fruit of 4 cocci. When polygamous, ♂ flowers with rudimentary stigmas and ovules, ♀ flowers without trace of stamens.

The vascular scheme of trunk cords as in *Haloragis* (see above), but both staminal whorls are usually without differentiated vascular elements. On the other hand, well-developed sterile carpel midrib bundles originate from the antepetalous trunk cords as the ovary wall becomes disjoined from the outer whorls, but the petal midribs are feebly developed. As the loculi close, giving place to four separate tracts of conducting tissue, the fertile carpel (placental) bundles divide in two. The resulting twin bundles diverge as in *Haloragis* (see above), so that each style receives three bundles, viz. the midrib of a sterile carpel flanked on each side by a bundle representing half the vascular system of the adjacent fertile carpel on the corresponding side. Splitting of the ground tissue of the fertile carpels from the centre outwards accompanies the division of the placental bundles, thus giving rise to the four sectors which continue upwards to form the separate styles. Extension of this splitting to the base of the ovary results in the formation of the four cocci of the fruit.

**Gunnera spp.** Flowers unisexual or polygamous (e.g. *G. manicata*), monœcious, considerably more reduced than in *Myriophyllum* (see above). Ovary always unilocular with a single ovule.



**G. manicata.** The subtending bract non-vascular. ♀ Flower. (Generally) K 2, median C o (rarely 1 or 2 lateral) A 2, lateral, stigmas 2, non-vascular, lateral; exceptionally, K 3 C o A 3, stigmas 2. In flowers which become ♂ the ovule is rudimentary, and the stigmas are greatly reduced or are absent altogether. In flowers which become ♀ the stamens no longer attain separate morphological form, but may still be represented by the two lateral vascular bundles which, however, cease before reaching the exertion level. They afford one of many instances where the vascular bundle persists after the corresponding floral member fails to attain distinct morphological form.

In the typical ♀ flower the single vascular strand entering the flower base gives rise to four cords only. These stand in the orthogonal planes. A branch detached shortly from one of the two median cords serves the ovule. Above this level both median cords continue upwards in the flower wall, turning outwards at the exertion level to become the sepal midribs. The two lateral cords similarly furnish the bundles for the petals when present (as in *G. petaloidea*) and the superposed stamens. From the fact that the two stigmas, which are non-vascular, lie in the same plane as the petals and stamens, it may be inferred that the corresponding sterile carpel bundles, now lost, when present, were detached from the same lateral cords as the petal and stamen bundles, hence the superposition of the three whorls. G will, therefore, be expressed as 2 lateral, sterile and 1 median, posterior, fertile, an anterior, fertile member having presumably been lost.

## 94. HIPPURIDACEÆ

Flowers borne singly in the axils of the several leaves of successive whorls, ♂, syngonous. Perianth reduced to a non-vascular sinuous rim probably representing four perianth members. Stamen one, anterior, with a vascular bundle. The gynæceum consists of a unilocular ovary and a short non-vascular style passing into a long cylindrical tapering stigma. Ovule solitary, pendulous from the top of the loculus. Fruit nut-like.

The single vascular strand which enters the flower base immediately forks. The anterior bundle passes into the stamen, the posterior one runs up on the opposite side in the ovary wall and serves the ovule. Hence the flower is terminal on the abbreviated axillary axis. So great a reduction in the vascular system renders it somewhat difficult to determine the number of carpels, whether one, or two of which the one is sterile and non-vascular the other vascular and fertile. The balance of evidence favours the latter interpretation ( $G = 2$ ). The main grounds for this conclusion are threefold. (1) Analogy with the Haloragaceæ (in which Family *Hippuris* was earlier included, see under that Family earlier in the present Volume, Part 8, p. 298). (2) Were the ground-plan represented by A 1 G 1 the single valve carpel must either be presumed to be terminal, an inadmissible construction in view of the known facts regarding the relations of angiosperm axis and leaf; or, if it is lateral and the axis terminates between stamen and carpel, the latter member would then have its back turned towards, and its meeting edges away from the axis, a position unknown in any other type. Whereas if  $G = 2$  the axis would terminate between the two carpels, the styled sterile carpel as well as the stamen being anterior, the styleless consolidated fertile carpel posterior, and the orientation normal.

Superposition of the sterile carpel upon the stamen would naturally result if this carpel midrib (now lost) and the stamen bundle had originally been conjoined in a common trunk cord. (3) Exceptional flowers have been recorded in *Hippuris* in which the number of stamens and carpels was doubled. The fact that in such flowers the stamens and carpels all stand in the median plane is difficult to reconcile with a *single* flower ground-plan of A 2 G 2. But on the supposition that in these exceptional cases bifurcation of the axis has taken place, such as occurs not infrequently in some Papilionatæ (see under Leguminosæ earlier in the present Volume, Part 5, p. 189) twinning would result and the orientation of the stamens and carpels and their relation to the twin axes would be the same as in the single flower borne by the undivided axis. On this interpretation the entire structure in the exceptional case represents not a single flower with two members in the whorl of the stamens and of the carpels in place of the normal one member, but twin flowers, each, so far as the andrœcium and gynœceum are concerned, with the ground-plan of a normal flower.

### ILLUSTRATIVE TYPES

**\**Hippuris vulgaris*** (Mare's Tail). See the characters of the Family.

## 95. THELYGONACEÆ

Flowers unisexual, monœcious. Perianth single, tubular below, segmented or lappeted above. ♂ Flower. Perianth cut into two or three segments or with four or five small lappets. Stamens 6, 8, 10 or up to 30 arranged in a single ring and springing from the perianth tube, monadelphous below. G o. ♀ Flower. Perianth tube at first completely enclosing the gynœceum, enlarging below as the ovary develops and becoming coherent with it; remaining narrow in the upper portion enclosing the style, with two median lips between which the style protrudes G 2 lateral, one sterile, in line with the style, one fertile.

Owing to bulging of the fertile carpel to accommodate the large ovule the apex becomes pushed sideways and downwards so that the style, originally terminal, becomes 'gynobasic.' Ovary unilocular. Style filamentous. Ovule solitary, basal. Fruit drupaceous.

## ILLUSTRATIVE TYPES

**Thelygonum Cynocrambe.** ♂ Flower. Perianth divided above into two or three segments which become rolled back when the flower opens. Stamens 8-30 in close contact in a continuous ring, sometimes cohering at the base. The flowers open and fall quickly, being detached whole from the slender pedicel. ♀ Flower. See the characters of the Family.

The vascular system at the base of the ♂ flower consists of a central cylinder of many (20-30) equal small bundles in close contact. A branch turning outwards is given off from several of these bundles. These branches furnish the veins of the perianth segments. It is not apparent in transverse section from which bundles they will arise. They are unequally spaced, and neither in size nor position are they recognisable as midribs and secondary veins. The veins on the segmentation radii sometimes (? always) give rise to

feeble commissural marginal veins in the free segments. The central vascular cylinder which at the base of the ♀ flower passes into the ovary consists of a small number of unequal-sized bundles. A slender bundle turns outwards on the one side and enters the style. The arc of stouter bundles on the opposite side supply the bulging wall of the ovary. From the inner face of this arc undifferentiated strands turn inwards and become 'condensed' into the bundle for the ovule. This configuration indicates the formation of the gynæceum from two carpels, one styled and sterile, the other styleless and fertile.

## 96. ARALIACEÆ

Plant with abundant secretory canals, generally accompanying midrib bundles, sometimes the finer veins also. Flowers in umbels, heads, spikes or racemes, generally ♂, syngonous, five-whorled through absence of an antepetalous stamen whorl, isomerous throughout or with an oligomerous gynæceum, sometimes with stamens several times as many as the petals through multiplication of the antesepalous staminal members. Ovary multilocular or very rarely unilocular through cessation of the central parenchyma; surmounted by a flat or convex crenate disc, formed of carpellary tissue and extending from the level at which the conjoined carpels become disjoined from the outer whorls to the base of the styles. Styles distinct, or connate with distinct stigmas. Ovules solitary in the loculi, pendulous from the summit of the ovary. Fruit with fleshy outer wall. Seeds enclosed in the (generally) cartilaginous endocarp (pyrenes).

A considerable range of variation occurs within the Family in the number of members in the whorls, indicating a general trend from a condition of unstable pleiomery to one of stability, as an increasing degree of sterility in the female organ and reduction in the ground-plan reach a maximum.

This trend is shown in the following series of selected grades :—

K an unsegmented rim C 10-15 A 10-15 G 10-15, sterile + 10-15, fertile (*e.g. Gastonia*).

K an unsegmented rim C 5-15 A 5-15 G 5-15, sterile + 5-15, fertile (*e.g. Schefflera*).

K an unsegmented rim C 10-12 A 10-12 G 10-12, sterile + 10-12, fertile (*e.g. Sciadendron*).

K 5-8 C 5-8 A 5-8 G 5-8, sterile + 5-8, fertile (*e.g. Pentalanax*).

K 5 C 5 A 5 G 10, sterile + 10, fertile (*e.g. Dizygotheca*).

K 5 C 5 A 5 G 5, sterile + 5, fertile (*e.g. Hederopsis*).

K 0 C 5 A 5 G 5, sterile + 5, fertile (*e.g. Fatsia*).

- K 5 C 5 A 5 G 5-3 + 5-3 ; when quadri- or trilocular ovule development not restricted to the antesepalous members (*e.g. Hedera*).
- K 5 C 5 A 5 G 5-2 + 5-2 ; when quadri-, tri- or bilocular ovule development not restricted to the antesepalous members (*e.g. Aralia*).
- K 5 C 5 A 5 G 5 + 5, bilocular, ovule development not restricted to the antesepalous members (*e.g. Cussonia, Heteropanax, Myodocarpus*).

The midrib bundles for all the whorls are derived from a single trunk cord on each of the construction radii (ten in the pentamerous type). Those on the sepal radii become resolved at the exsertion level into sepal midrib (if the calyx is vascular), antesepalous stamen bundle and fertile carpel midrib bundle (if present). Those on the petal radii yield at the flower base in a few types a pair of sterile carpel laterals, and at the exsertion level petal midrib and sterile carpel midrib. The placental system of the fertile carpels is differentiated at varying levels from the central ring of residual vascular elements delimited from the out-turning trunk cords at the base of the flower. This system consists of a varying number, corresponding with the number of loculi, of twin placental bundles on the sepal radii which are used up in providing the bundles for the ovules.

Since the number of individual placental strands is twice that of the loculi, and since only one ovule is developed in any loculus, it follows that there must always be some placental strands which do not function. The distribution of the ovules among the placentæ appears to be quite irregular and to be determined by the particular conditions obtaining in individual flowers. Thus, in quinquelocular ovaries, both the placental strands of one or of two carpels may serve ovules, and both the placental strands of two other carpels, or of one, may be sterile. Or one strand of one or of more than one carpel may be functional and the other sterile. The only constant relation between placentæ and ovules is the development of one ovule in every loculus. (See also earlier in the present Volume under Malpighiaceæ, Part 6, p. 199.)

Among types with a pleiomerous gynæceum, *Dizygotheca* stands alone in also showing duplication of the antesepalous stamen whorl (see above), a feature rendered obvious to the eye, however, only by the thick filaments and double anthers, since the pair representing each member are fused throughout.

In those flowers in which the number of carpels which develop ovules (and therefore also the number of the

loculi) is less than the number of members in a perianth or stamen whorl ovule formation is not restricted to the carpels on one set of radii. As in those flowers in which such numbers correspond the fertile carpels occur on those of the construction radii which provide the nearest approach to equal spacing. Hence it follows that in quadri-, tri-, and bilocular ovaries, at least one ovule-bearing member will be antepetalous. It is obvious from this plan of distribution that in both the quadrilocular and the trilocular ovary the several ovule-bearing carpels will be separated by an unequal number of radii on which the carpels will be without ovules. In this kind of irregular symmetry arising from reduction the number of trunk cords from which carpel midrib bundles are detached varies. They may be formed on all the intervening radii or only on some according to the vigour of the individual. In the trilocular and quadrilocular gynæcea of types having connate styles but distinct stigmas it follows, since the stigma lobes are centred between the fertile carpels, that the stigmatic lobes will vary in thickness, as can commonly be seen in *Hedera* (Ivy).

From the foregoing facts it becomes clear that in araliaceous flowers with a pentamerous perianth and andrœcium and a quadri- or trilocular ovary the anatomical relations of the gynæceum are comparable with those observable in exceptional flowers of *Saxifraga* which are four- or three-styled; and that in araliads with a bilocular ovary they are similarly comparable with those obtaining in the normal two-styled *Saxifraga* flower (see earlier in the present Volume under Saxifragaceæ, Part 5, p. 153).

Genera in which the gynæceum is regularly bilocular (e.g. *Cussonia*, *Heteropanax*, *Myodocarpus*, *Delarbrea*) show almost complete similarity with those Umbelliferæ in which the characteristic prolongation of the axis between



the two halves of the fruit is absent or negligible in extent, as in species of *Hydrocotyle* (see later in the present Volume, Part 8, p. 314). This likeness may indeed be said to be complete in *Myodocarpus*, for in this latter genus the fruit splits in half into two one-seeded portions.

In the few genera with a unilocular gynæceum (*Arthrophyllum*, *Eremopanax*, *Crepinella*) reduction is carried to the limit. The tissue of the axis comes to an end at the flower base. Only one carpel is fertile, the solitary ovule hangs from the top of the wall of the ovary, and the loculus is undivided.

### ILLUSTRATIVE TYPES

**Fatsia japonica.** K 0 C 5 A 5 G 5, sterile + 5, fertile. Ovary quinquelocular. Styles and stigmas distinct, 5, centred over the sterile carpels, each representing  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels.

The vascular ground-plan is diagrammatically regular owing to the presence of a large amount of central parenchyma, to the delimitation of the placental bundles of the fertile carpels at the base of the flower, and to the formation and persistence of a primary pair of lateral veins of the sterile carpels which are detached from the petal-carpel trunk cords as soon as they turn out from the central cylinder. The fertile carpels lack a midrib bundle. The sterile carpel midribs come to an end as the loculi close, but the primary laterals continue. As they turn inwards to the style column the pair belonging to each sterile carpel pick up one of the two placental strands of the neighbouring fertile carpel on each side. Hence the styles which stand over these reconstructed pairs of bundles correspond to one whole sterile carpel together with half the fertile carpel on each side.

**Acanthopanax spp.** (e.g. *A. Sieboldianum*). K 5 C 5 A 5 G 5, sterile + 5, fertile. Ovary quinquelocular. Styles 5, connate below, free above, centred over the sterile carpels.

Sterile carpel primary lateral veins and fertile carpel

placental strands formed as in *Fatsia japonica* (see above), but the whole systems of both sterile fertile carpels prolonged into the style column.

As the stamen bundles separate from the cords on the sepal radii (the sepal midrib bundles having already been detached from these cords at a lower level) the residual portion of each cord, representing a fertile carpel midrib is split in half. As the loculi close the two strands of each pair turn inwards and pick up the corresponding pair of placental bundles. The resulting twin bundles (= the whole system of one fertile carpel) then diverge and fuse, respectively, with the sterile carpel midrib on each side. The five vascular units so formed are continued into the style column, one unit passing into each stigmatic arm which thus represents  $\frac{1}{2}$   $\times$   $\frac{1}{2}$  carpels.

**Aralia spp.** (e.g. *A. californica*, *A. chinensis*). K 5 C 5 A 5 G 5, sterile + 5, fertile. Ovary quinquelocular. Styles 5, connate. Style column fluted through partial median radial splitting of the fertile carpels from without inwards. Stigma lobes 5, distinct, centred over the sterile carpels. Sterile carpel midribs without the pair of primary lateral veins present in *Fatsia* and *Acanthopanax* (see above). Placental bundles of the fertile carpels organised at the base of the flower (*A. chinensis*) or towards the top of the ovary (*A. californica*). Above the level at which the stamen bundles become free the carpel vascular system shows the same features as in *Acanthopanax* (see above), but the sterile carpel midribs soon cease to be traceable in the style column. Hence each of the five component styles, though corresponding to  $\frac{1}{2}$   $\times$   $\frac{1}{2}$  carpels, shows two separate bundles corresponding to half the vascular system of each of two neighbouring fertile carpels.

**\*Hedera Helix** (Ivy). K 5 C 5 A 5 G 5-3 + 5-3. Ovary with 5-3 loculi. Ovule formation in the oligomerous gynæceum not restricted to the carpels on one set of radii. Styles connate. Style column short, cylindrical, terminating in 5-3 stigmatic lobes.

The vascular ground-plan of the gynæceum is more complex and less regular than in the preceding genera. This is due to an irregular system of secondary veins in the wall of the ovary, to anastomosis between the carpel systems, and to reduction to a minimum of the central parenchyma with the result that delimitation of the

placental systems sometimes only becomes complete near the top of the ovary. When the ovary is quinquelocular the number and functional relations of the carpels and the main features of the vascular scheme agree with those of the preceding types (see above). When the number of loculi is reduced to four or three a different set of relations is set up as described in the general account of the Family (see above).

**Cussonia spp.** K 5 C 5 A 5 G 5 + 5. Ovary bilocular. Styles 2, standing in the median plane, each formed of five carpels. Only two carpels standing opposite to one another are fertile, one being antesealous, the other antepetalous. Thus here, as in the tri- and quadrilocular ovaries of *Hedera*, ovule formation is not restricted to the carpels situated on one set of radii. Each of the usual ten primary trunk cords, as it becomes resolved into its components, gives rise to a carpel bundle corresponding to a midrib. The two placental bundles, are delimited, as in *Fatsia*, at the base of the flower (see above). They belong to one of the two carpels lying nearest to the lateral plane on the dorsal side and to one of the corresponding two on the ventral side of this plane. In these respects *Cussonia* offers a precise parallel with the Umbelliferæ (see later under that Family, Part 8, p. 310), and also, except for the solitary ovules, with the typical two-styled flower of *Saxifraga* when full carpel development takes place (see under Saxifragaceæ, *loc. cit.*).

## 97. UMBELLIFERÆ

Plant with abundant secretory canals. The termination of the peripheral tissues of the pedicel beneath the flower often so sharply marked as to appear as an articulation. Flowers rarely in simple, generally in compound, umbels, usually ♀, sometimes through abortion unisexual or polygamous (*e.g.* *Echinophora*, *Hacquetia*, *Petagnia*, *Astrantia*), rarely diœcious (*e.g.* *Arctopus*), syngonous, five-whorled as in Araliaceæ (see earlier in the present Volume, Part 8, p. 303) through absence of an antepetalous stamen whorl, generally isomerous and pentamerous (K 5 C 5 A 5 G 5 + 5) (3, pp. 152–154†). Sepals usually in the form of small, often non-vascular teeth or merely forming a rim on the top of the ovary, rarely well-developed with conspicuous midrib (*Astrantia*, *Eryngium*). Petals of the flowers at the circumference of the umbels sometimes of unequal size. Ovary surmounted by a conspicuous bilobed disc, the two lobes being formed of an enlargement of the two quintuplets of carpels forming the two halves of the gynœceum which contract above to form the styles. Styles 2, standing in the median plane. Ovary often with ten prominent ribs corresponding with the radii of the ten perianth members, and with secretory canals on the intervening radii which become conspicuous in the fruit (*vittæ*); bilocular with a transverse partition. Four of the ten carpels alone are potentially fertile, *viz.* each of the two lying nearest the lateral plane in the anterior and in the posterior half. But of these four only two bear a fully developed ovule. If the carpel on the right is fertile in the anterior half the one on the left in the posterior half is usually the other, and *vice versa*. Ovules solitary in the loculi, suspended from the top of the ovary. The Umbelliferæ have thus reached as a Family a stable condition of maximum reduction in fertility combined

with symmetrical construction in the gynæceum, a condition which the Araliaceæ are also approaching, but which in that Family has been attained only by the small number of genera having a bilocular ovary (see earlier in the present Volume, Part 8, p. 308).

The ground tissue of the axis is generally prolonged between the two groups of carpels forming together with the placentæ the transverse partition, as in Aceraceæ (see under that Family earlier in the present Volume, Part 6, p. 222). The core of this tissue becomes sclerosed, forming a tract of lignified elements which forks before coming to an end. As the fruit ripens the unlignified ground tissue dries up and the anterior and posterior halves of the gynæceum, now separate, hang suspended from the two ends of the sclerenchymatous support (carpophore) as two one-seeded partial fruits (mericarps). In the few genera in which the axis is not prolonged the ripe mericarps remain attached at the base but separate above this level along their length. In other genera in which a carpophore appears to be absent, as *e.g.* *Astrantia*, a tract of carpophore tissue is, in fact, present, but so deeply is it constricted in the lateral plane that when the fruit is ripe the narrow connecting neck is easily snapped. The now separate longitudinal halves of the carpophore are left adherent throughout their length to the two mericarps which remain attached at the base instead of hanging free from the two ends of a single intact and detached carpophore.

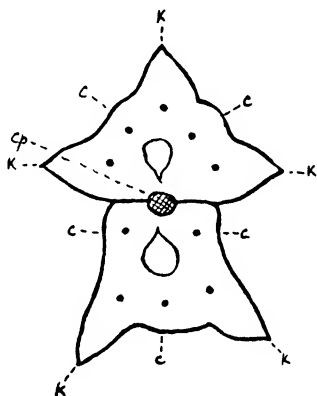
As in general in more or less syngonous types (*e.g.* Araliaceæ and Saxifragaceæ, see earlier in the present Volume, Part 8, p. 304, and Part 5, p. 144, respectively) the vascular bundles for all the whorls are derived from a single trunk cord on each of the construction radii. Those on the sepal radii furnish the sepal midribs, antesealous stamen bundles and a carpel component, those

on the petal radii the petal midrib bundles and a carpel component. As the sepals, petals and stamens become free and the loculi become roofed-in the remaining components of the quintuplet of cords in each half of the gynæceum turn inwards. In some genera (*e.g. Smyrniium*) these carpel bundles merge into a single strand which ceases to be traceable beyond the style base. In others (*e.g. Astrantia*) each style has two bundles, the pair in each filament representing the two carpels standing next the partition on the corresponding side, of which one bears an ovule. Exceptionally (as in *Arctopus*, see later, p. 312), each style has three vascular strands. Two represent the same carpels as in *Astrantia*, the third the combined bundles of the three, always sterile, carpels on the other radii on the corresponding side of the lateral plane. A placental branch is detached from one, or more generally from both of the primary cords lying next to the transverse partition in each half of the gynæceum at varying levels, below the level of the loculi in *Hydrocotyle spp.* without a carpophore, at the summit of the ovary in *Smyrniium*, a genus with a carpophore. These branches end at the ovule level.

It follows from the relations described above that the two mericarps are not anatomically precisely alike, since the one is a structure with the external features characteristic of the radii of three sepals and two petals and the other with those of two sepals and three petals. This structural diversity becomes appreciable in those types which show a marked difference in the prominence of the ribbing on the radii of the sepals and petals, respectively, such as occurs in *Elæoselinum Asclepium*, which is strongly ribbed only on the sepal radii; hence the one mericarp is always three-winged and the other two-winged (see Fig. 11).

Inequality in the two mericarps may also occur when the

size of the ribs is not strictly related to alternate (sepal and petal) radii, as in *Molopospermum cicutarium* (see Pflanzenfamilien III, 8, Umbelliferae, p. 96, Fig. 36A). Or again, it may follow from an accidental irregularity. In a flower of a species of *Hydrocotyle* lacking a carpophore, an inequality in the spacing of the ten original trunk cords resulted in six carpels being incorporated in one mericarp and four in the other (unpublished). When such unequal halving occurs the ovule-bearing function must necessarily be taken on by one carpel which is normally sterile, and one which ordinarily is fertile becomes sterile.



*Elaeoselinum Asclepium*. The ovary in transverse section showing a trunk cord on each sepal (*K*) and each petal (*C*) radius, the two loculi and the carpophore (*cp*). (For the explanation of the unequal size of the two mericarps see the text.)

FIGURE II.

In the unisexual and dioecious species *Arctopus echinatus*, the ♀ flower in which the andræcium is entirely suppressed is exceptional in that only one ovule is developed. The posterior half of the ovary remains solid until near the top when a small cavity makes its appearance; but no placental strand is developed. The carpel bundles continue into both styles, each receiving three separate stands as in *Astrantia* (see above). In the ♂ flower there is no structure corresponding to an ovary. The only recognisable gynæceal tissue is a small disc with two minute processes representing reduced styles. This tissue is non-vascular, the whole of the original ten trunk cords being used up in supplying the perianth and andræcium.

The Umbelliferæ show a likeness to the Aceraceæ in that the ovary in both Families is divided in half by a central prolongation of the axis tissue so that in the fruit the two halves (the samaras of *Acer* and the mericarps of the Umbellifer) hang from the two forks in which the prolongation ends. (See earlier in the present Volume under Acceraceæ, Part 6, p. 222.) Furthermore, although the normal flower in both Families is two-styled, three-styled flowers which are of frequent occurrence in *Acer* are occasionally formed in many Umbelliferæ, notably in *Smyrnum Olusastrum*. But here the resemblance ends, for there is a profound difference in the way in which the pleiomerous gynæceum comes into being in the two Families. In the hypogynous or slightly perigynous normal two-styled flower of *Acer* the residual vascular tissue supplying the andrœcium and gynæceum consists of a ring of ten cords lying within the disc on the ten construction radii. Strands detached from the inner face of these cords give rise to the vascular systems of the two carpels present. In the three-styled flower there may be no alteration in the perianth-stamen ground-plan. The only difference between the two flowers lies in the organisation of the strands detached from the residual ring of ten cords into three carpel systems instead of two, and the associated splitting of the prolongation of the axis into three at the top. In the syngonous flower of the Umbelliferæ a single vascular cord on each of the ten construction radii serves all the members present on each corresponding radius. An addition to the number of carpels is necessarily accompanied by at least a corresponding increase in the number of members of the perianth and also probably by some increase in the number of stamens. In other words, in the three-styled flower there occurs a fundamental change of ground-plan resulting in an increase in the number of construction



radii. According as the number of these additional radii on which development takes place is three, four or five, the additional third mericarp will be composed of three, four or five carpels. An additional style will be formed and the prolongation of the axis will divide above into three.

### ILLUSTRATIVE TYPES

**\*Heracleum Sphondylium** (Cow Parsnip). Sepals forming distinct teeth. Mericarps with conspicuous vittæ but ribs little prominent. Carpophore split down the greater part of its length.

**\*Scandix Pecten-Veneris** (Venus's Comb). Calyx scarcely defined. Gynæceum with long beak and carpophore which forks only at its extremity.

**\*Hydrocotyle vulgaris** (Marsh Pennywort) (3, p. 152, Fig. 64). Calyx scarcely defined. Carpophore absent. Placental vascular strands formed below the loculi. Mericarps separating along their length but remaining attached by the base until shed.

**\*Smyrniololusastrum** (Alexanders). Calyx scarcely defined. Carpophore present but not reaching to the summit of the ovary; hence the loculi become continuous below the level at which the styles roof-in the cavity. Placental strands developed at the top of the ovary. Exceptional flowers with more than five sepals and petals and with three mericarps and a tripartite carpophore not infrequent.

## 98. CORNACEÆ

Flowers generally ♂ (*e.g. Cornus, Corokia*), sometimes unisexual and dioecious (*e.g. Aucuba, Griselinia*), syn-gonous, actinomorphic, isomerous throughout or with an oligomerous gynæceum (*e.g. Corokia*), tetramerous or pentamerous. When ♂ five-whorled as in Araliaceæ and Umbelliferæ (see earlier in the present Volume, Part 8, pp. 303 and 309, respectively) through absence of an antepetalous stamen whorl; or four-whorled when, in addition, sterile and fertile carpels are disposed in a single whorl (*e.g. Cornus*). Calyx reduced to mere teeth or scarcely defined; teeth, when four, in the orthogonal planes. Petals valvate; when four, in the diagonal planes. A carpellary disc between the exsertion level of the outer whorls and the style base as in Araliaceæ (*loc. cit.*, p. 303), rarely in the form of an enlargement of the style base as in Umbelliferæ (*loc. cit.*, p. 309). Ovary generally uni- or bilocular, seldom tri- or quadrilocular. Styles generally connate, rarely distinct. Stigma entire or with as many lobes as there are loculi. Ovules solitary in the loculi, pendulous from the top of the ovary as in Araliaceæ and Umbelliferæ (*loc. cit.*, pp. 303 and 309, respectively). Fruit generally drupaceous, the 'stone' (pyrene) with 1-3 loculi and 1-3 seeds; sometimes baccate and one-seeded.

## ILLUSTRATIVE TYPES

**Aucuba japonica** (Variegated Laurel). Flowers dioecious, generally tetramerous. ♂ Flower without trace of a gynæceum beyond a central disc. K 4 (non-vascular) C 4 A 4. ♀ Flower without trace of an androecium. K 4 (non-vascular) C 4 G 8, the posterior antesepalous member alone fertile. Disc without the veins present in some genera (*e.g. Corokia*). Style single, ending in a

large, oblique, grooved, zygomorphic stigma. Fruit baccate, one-seeded.

As in general in syngonous types, all the whorls are served by a single trunk cord on each of the (here eight) construction radii. In the ♀ flower those on the sepal radii furnish only the bundles of the antesepalous carpels since the sepals are without vascular tissue; those on the petal radii supply the petal midribs and the bundles of the antepetalous carpels. All the eight carpel bundles are prolonged to the top of the style. The funicle strand of the solitary ovule is derived from the posterior (antesepalous) carpel bundle. As the ovule enlarges and fills the locus the bundle of this fertile carpel and that of the adjacent sterile antepetalous carpel on the right or left are forced apart. Above the ovule the locus narrows to the slit-like stylar canal which is extended obliquely, lying in the intermediate plane between the orthogonal plane occupied by the fertile and the opposite antesepalous carpels, and the diagonal plane occupied by the displaced and the opposite antepetalous carpels. The canal opens to the surface at that end of the slit nearest the above-mentioned wide gap between two of the carpel bundles; hence the resulting groove (= the plane of symmetry) cuts the median plane of the flower at an angle, the eight bundles being grouped round the other end of the canal in the form of a horseshoe. The eight-carpelled stigma is thus turned obliquely and in its outline simulates the appearance characteristic of many types in which it is formed of 1 or of  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels (see e.g. under *Actæa* among Ranunculaceæ in Vol. I, Part 2, p. 37).

**\*Cornus** (Cornel, Dogwood). Flower ♂, tetramerous, isomerous, K 4 (non-vascular) C 4 A 4 G 4, the two median carpels sterile, the two lateral fertile. Variations from the type occur occasionally in the form K 5 C 5 A 5 G 6 (3 sterile and 3 fertile) and K 3 C 3 A 3 G 4 (2 sterile and 2 fertile). In the tetramerous type both stamens and carpels are superposed on the sepals, the bundles for these two vascular whorls being derived from a single set of four trunk cords, the four cords on the alternate radii giving rise only to the petal bundles. Resolution of the stamen-carpel trunk cords into their two components takes place below the level of the loculi. Ovary bilocular, the fertile carpels forming the partition. Sterile carpel

bundles feebly developed. Style single without differentiated vascular tissue. Stigma simple or obscurely bilobed and then isobilateral. Fruit drupaceous with two loculi and two 'stones' (pyrenes).

**Corokia spp.** (*e.g.* **C. macrocarpa**, **C. virgata**). Flower ♂, generally pentamerous with an oligomerous gynæceum. K 5 C 5 A 5 G often 3, sometimes more or fewer, never more than one fertile. Terminal flowers occasionally hexamerous with four carpels. Ovary unilocular. Style single with as many vascular bundles and stigma lobes as there are sterile carpels. Fruit drupaceous with one pyrene.

The vascular system of the perianth is unusually well-developed. The (in pentamerous flowers) ten primary cords give rise to anastomosing secondary veins, those formed at the exertion level of the perianth turning inwards and ending blindly in the tissue of the disc. The sepals possess a midrib and also commissural marginal veins.

The spacing of the sterile carpels is both unequal and inconstant. When, for example, only two are developed, they may stand on near-by radii. This irregularity may be due in part to the fact that the ten primary cords are not equally spaced at their origin for not all arise separately. Some are combined in pairs, or even in triplets, which later become resolved into their components. These disjoined cords then diverge and occupy their proper radii. It may well be that the conditions which determine on which radii the carpels will be developed are thus operative sometimes before resolution of the separate trunk cords into their components takes place.

## 99. GARRYACEÆ

Flowers unisexual and dioecious, ordinarily tetramerous, but ♂ flowers which are terminal sometimes pentamerous. ♂ Flower. T 4, valvate A 4 G wholly absent or represented by a remnant of disc tissue. ♀ Flower. T 0 A 0 G 4, 2 sterile, 2 fertile. Ovary unilocular. Ovules 2, pendulous from the top of the ovary as in Cornaceæ, Umbelliferæ and Araliaceæ (see under these Families earlier in the present Volume, Part 8, pp. 315, 309, and 303, respectively). Styles 2, standing over the sterile carpels, stigmatic on their inner face. Fruit a 1-2-seeded berry.

## ILLUSTRATIVE TYPES

**Garrrya elliptica.** ♂ Flower. Tepals with an unbranched midrib. A minute remnant of disc tissue generally present. ♀ Flower. Ovary flattened so that the diameter of the loculus is greatest in the plane of the fertile carpels. As the loculus contracts to the stylar canal the narrow, slit-like canal remains extended in the same plane. Above the ovule level the fertile carpel bundles divide in half and diverge. As the canal opens to the surface in the plane of compression the styles separate, and hence are stigmatic over the whole inner face. Each style receives a sterile carpel midrib and half the vascular system of the fertile carpel on each side, hence each corresponds to  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels.

## Part 9

### Dicotyledons

Family	100.	Saururaceæ
„	101.	Piperaceæ
„	102.	Salicaceæ
„	103.	Juglandaceæ
„	104.	Myricaceæ
„	105.	Betulaceæ
„	106.	Fagaceæ (Cupuliferæ)
„	107.	Ulmaceæ
„	108.	Moraceæ
„	109.	Urticaceæ
„	110.	Proteaceæ
„	111.	Santalaceæ
„	112.	Loranthaceæ
„	113.	Aristolochiaceæ



## 100. SAURURACEÆ

Flowers in catkin-like spikes with a subtending bract but without bracteoles and without perianth, ♂, hypogynous or syngonous. Stamens in two tri- or tetramerous whorls or fewer through suppression. Carpels in two, generally 3- or 4-merous, sometimes 5- or 6-merous whorls. Ovary syncarpous and unilocular or multilocular through fusion of the fertile carpels with the central parenchyma of the axis, but very shortly becoming pseudo-apocarpous through median radial splitting of the fertile carpels from without inwards. Ovules in two or more rows in each loculus. Styles distinct, standing over the sterile carpels, stigmatic on the inner face. Fruit baccate or a collection of follicles.

### ILLUSTRATIVE TYPES

**Houttuynia cordata.** Flower partially syngonous. A (generally)  $3 + 0$  sometimes  $3 + 3$  (or more through multiplication), becoming free from the gynæceum about half way up the ovary G 3, sterile, superposed upon the outer stamens + 3, fertile, on the alternate radii. Ovary unilocular; as it passes into the three styles the fertile carpels become split radially in half so that each style consists of a sterile carpel conjoined with half the adjacent fertile carpel on each side ( $\frac{1}{2}$  &  $\frac{1}{2}$ ). Ovules in several rows on each fertile carpel. Fruit opening between the styles.

The vascular unit which supplies the flower generally breaks up in the first instance into only four cords, of which one immediately breaks up further into three cords. These six cords take up their positions on equidistant radii. Three give rise to the bundle of an outer stamen and to the midrib of a sterile carpel, the alternate three (in the *fully developed* flower) to an inner stamen bundle and the placental bundle of a fertile carpel. As the stamen and carpel bundles thus



arise conjoined together, the suppression of the inner staminal whorl in the  $A\ 3 + 0$  flower will not affect the radial position of the succeeding carpel whorl. As the loculus begins to close the fertile carpel bundle divides in half. The two resulting bundles diverge and fuse, respectively, with the neighbouring sterile carpel bundle on each side. Hence each style receives the whole vascular system of a sterile carpel and half the vascular system of the fertile carpel in each side.

**Saururus cernuus.** Flower hypogynous.  $A\ 3 + 3$  or sometimes 7 or 8  $G\ 4$  (or 5 or 6), sterile + 4 (or 5 or 6), fertile. Ovary soon becoming pseudo-apocarpous through median radial splitting of the fertile carpels from without inwards. Loculi 4 (or 5 or 6). Ovules 2-4 in each loculus, standing two abreast. Fruit separating into 4 (or 5 or 6) cocci through completion of the splitting of the fertile carpels.

The vascular tissue at the base of the gynæceum consists of as many bundles as loculi situated on the radii of the loculi in a ring round the central parenchyma of the axis. The middle portion of each of these bundles turns outwards to become the midrib of a sterile carpel, leaving a residual portion behind on each side. Owing to the premature radial splitting on the intervening radii the adjacent residual portions of these bundles representing the two placental strands of a fertile carpel do not converge, as ordinarily, on the intervening radius, but remain apart, the line of fission passing between them as the split becomes complete. That the pairs of these residual strands alternating with the sterile carpel midrib bundles nevertheless represent the vascular system of an alternate whorl of fertile carpels, and that the gynæceum is not truly apocarpous but pseudo-apocarpous, is confirmed directly by the continuity of the tissues of the ovaries in whole, or in part, until maturity, and indirectly by analogy with *Houttuynia*.

## 101. PIPERACEÆ

Flowers in catkin-like spikes, with a subtending bract but without bracteoles and without perianth, ♂ or unisexual and then generally dioecious. When ♀ hypogynous. Stamens 6–2 in one or two di- or tri-merous whorls or reduced to 1. Carpels 6–2, sterile + 1, fertile (see below). Ovary always unilocular. Style when present single. Stigmas distinct, standing over the sterile carpels, but owing to unequal development or spacing, or to the dissimilar form of these carpels, often fewer than the carpels and unequal in size. Ovule solitary, basal. Fruit usually a berry.

The analysis of the gynæceum is rendered difficult owing to 'condensation' in the vascular scheme, but the manner of origin of the strand to the ovule in types in which it reaches an appreciable length favours the view that this strand is not a placental bundle derived from one of the carpels forming the wall of the ovary, but represents all that persists of the vascular system of the one surviving carpel of an inner whorl.

## ILLUSTRATIVE TYPES

**Macropiper spp.** Flowers unisexual, dioecious. ♂ Flower. A 2 or 3. ♀ Flower. G 6–2, sterile + 1, fertile. Stigmas 4–2 sessile (see below). These variations in number occur quite irregularly in the same inflorescence.

After the vascular bundle for the subtending bract has been given off from the single trunk cord which supplies each flower this cord breaks up simultaneously, or nearly so, into 6–2 bundles which radiate outwards and pass up in the wall of the ovary and a single central bundle which runs straight on to the ovule. When only 2, 3 or 4 sterile carpel bundles are formed they are usually equally spaced and equally developed and the ovary is crowned with a corresponding number of stigmatic rays. When 5 or 6 such bundles are formed they are usually unequally

spaced, one or two being weaker than the others. These weaker bundles either cease below the top of the ovary or converge towards a neighbouring strong bundle so that the corresponding stigmas become confluent. Hence the stigmas are sometimes of unequal size and fewer than the carpels, being never more, probably, than four.

The vascular bundles for the sterile carpels and the strand to the ovule, which is of considerable length, arise at about the same level from an irregular nodal complex.

**Piper spp.** (e.g. *P. umbellatum*) (Pepper). Flowers unisexual, diœcious. ♂ Flower as in *Macropiper* (see above). ♀ Flower. G (generally) 2, sterile + 1, fertile. Stigmas 2.

The vascular bundles for the carpels and ovule arise as in *Macropiper* (see above).

**Peperomia.** Flower ♀. A 2, lateral G 2 median, sterile + 1, fertile. The loculus is continuous above with the exterior by a narrow channel which is covered by the sessile stigma. This is central when the anterior and posterior carpels are of equal height, inclined towards the front when the posterior member overtops the anterior one.

**P. peltifolia, P. pellucida.** Stigma(s) terminal. The cells lining the channel to the exterior give rise either to a single central hemispherical tuft of papillæ or, if the opening widens out, the papillæ may be divided through a transverse depression into two median tufts, one over each carpel (*P. peltifolia*).

**P. Langsdorffii.** Stigma slightly oblique owing to slight overtopping of the anterior carpel by the posterior one.

**P. resedæflora, P. magnoliæfolia, P. incana.** Stigma anterior. The tuft of papillæ faces to the front, the posterior carpel being prolonged above into a style-like filament which is non-receptive.

A single trunk cord from the vascular system of the axis of the spike supplies each flower and its subtending bract. After the bundle for the bract has been detached the cord continues upwards to the flower base. Here at a nodal point it breaks up into the bundles for the two stamens and for the anterior sterile carpel. No bundle passes up in the posterior wall of the ovary, and in the flowering stage at least the very short funicle may be without a differentiated bundle. The variations in form and position of the stigma nevertheless indicate that, as in *Piper*, where a posterior as well as an anterior bundle are present in the ovary wall, two sterile carpels are present (see above). It is to be noted that a monocarpellary construction would be contrary to all experience, since the ovule must then be held to spring from the dorsal side of the loculus, for the only vascular bundle present runs up the dorsal mid-line of the ovary.

## 102. SALICACEÆ

Inflorescence catkin-like, many-flowered. The bract subtending each flower entire (*Salix*) or dentate or pinnatifid (*Populus*). Flowers diclinous and diœcious, without perianth and without trace of the other sex. Disc present; in *Salix* in the form of a single nectariferous process (posterior), or of two separate processes (anterior and posterior), or of an inconspicuous ring; in *Populus* forming a cup-shaped structure. ♂ Flower. Stamens 2-∞. ♀ Flower. Ovary syncarpous, unilocular, of 4 carpels, 2 lateral sterile, 2 median fertile. Ovules in several rows on each fertile carpel. Style single, of varying length, frequently so short that the stigmas are almost sessile, forking above into two stigmatic arms which remain entire (stigmas 2) or become bilobed or deeply forked (stigmas 4). Fruit a capsule splitting in the mid-line of the sterile carpels into two valves, each of  $\frac{1}{2}$  ♂  $\frac{1}{2}$  carpels. Seeds ∞ with a basal tuft of cottony hairs.

## ILLUSTRATIVE TYPES

**\*Salix** (Willow). Stamens generally few, often 2, sometimes 3 or 5.

**\*S. Caprea** (Sallow Willow). Nectary 1, posterior. ♂ Flower, A 2, lateral. ♀ Flower. Style very short. Stigmas 2, centred over the fertile carpels ('commisural').

As the style forks to form the two separate stigmas the sterile carpels split radially in half. Each stigma thus comes to consist of a fertile carpel flanked by half a sterile carpel on each side ( $\frac{1}{2}$  ♂  $\frac{1}{2}$ ).

Early flowers occasionally develop a multicarpellary gynæceum (G 3-6, sterile + 3-6, fertile, with 3-6 stigmas).

In the rare flowers which are ♀ the two stamens are lateral as in the ♂. The median carpels then become sterile and the lateral carpels fertile.

\***S. alba** (Common Willow). Nectaries 2, one anterior, one posterior. ♂ Flower. A 2, lateral. ♀ Flower. Style short. Stigmas 4, owing to the two stigmatic arms becoming bilobed. The two primary arms arise as in *S. Caprea* (see above) and consist of  $\frac{1}{2}$  +  $\frac{1}{2}$  carpels. These arms become bilobed through later splitting in half of the fertile carpel. Hence each stigmatic lobe consists of half a sterile and half a fertile carpel ( $\frac{1}{2}$   $\frac{1}{2}$ ).

\***Populus** (Poplar, Aspen). Disc in the form of a cup. ♂ Flower. Stamens numerous. ♀ Flower. Style short. Stigmatic arms 2, centred over the sterile carpels, each consisting, through median radial splitting of the fertile carpels, of a sterile carpel flanked by half a fertile carpel on each side ( $\frac{1}{2}$  +  $\frac{1}{2}$ ), often bilobed through later splitting in half also of the sterile carpel. The order of splitting of the two sets of carpels is thus the reverse of that in *Salix alba* (see above), though the final result (4 stigmas of  $\frac{1}{2}$   $\frac{1}{2}$  carpels) is the same.

## 103. JUGLANDACEÆ

Flowers unisexual through abortion, monœcious, almost always in different catkin-like spikes. T 4 (or 5, or fewer through suppression). ♂ Flower. A few- $\infty \pm$  G rudiment. ♀ Flower syngonous. G 4, either 2 median sterile, 2 lateral, of which only one is fertile, or the sterile pair lateral, the actually and the potentially fertile carpels median. Ovary unilocular, but owing to the protrusion inwards of the carpel midribs after pollination often with two or four incomplete partitions in the fruiting stage. Ovule solitary, basal, only attaining development after pollination. Style single, short. Stigmas 2, either broad, or forked and filamentous, sometimes centred over the sterile carpels, sometimes over the fertile carpels ('commissural'). Fruit a drupe or nut.

## ILLUSTRATIVE TYPES

**\*Juglans** (introduced) (Walnut). ♂ Inflorescence catkin-like, pendulous with  $\infty$  flowers borne singly. ♂ Flower. A 8- $\infty$ ; without G rudiment. ♀ Inflorescence erect with few flowers borne singly. ♀ Flower. Sterile carpels median. Stigmas broad, centred over the sterile carpels. Ovary generally with four incomplete partitions.

The two halves of the fruit shell (endocarp) separate by cleavage in the mid-line of the sterile carpels, hence each half does not correspond with a whole sterile carpel but with a fertile carpel flanked on each side with half of one of the median sterile carpels.

**Carya** (Hickory). ♂ Flower. A 3-10. ♀ Flower. Sterile carpels lateral. Stigmas broad, centred over the fertile carpels ('commissural'). Ovary with two or four incomplete partitions.

## 104. MYRICACEÆ

Flowers unisexual, monœcious or diœcious, when monœcious both sexes in the same inflorescence, generally in short, simple, compact spikes, without perianth and without rudiments of the non-functional sex. ♂ Flower. A 4, orthogonal (less often 2, 3 or 6–16). ♀ Flower. G 2, median, sterile + 1, fertile, or ? + 2 potentially fertile of which only one functions (see below). Ovary syncarpous, unilocular. Stigmas 2, filiform, formed by the sterile carpels but through torsion coming to stand in the lateral plane, receptive down their inner face. Ovule solitary, basal, erect. Fruit one-seeded, drupaceous.

## ILLUSTRATIVE TYPES

**\*Myrica Gale** (Bog Myrtle). Flowers diœcious, the ♂ subtended by a bract, the ♀ by a bract and a pair of bracteoles which adhere to the fruit. ♂ Flower. A 4. ♀ Flower. See the characters of the Family.

The vascular bundles which become the midribs of the two sterile carpels turn upwards in the median plane at the base of the gynæceum leaving behind a large solid central complex which serves the single ovule. This arrangement affords no clue as to whether this complex corresponds with two potentially fertile carpels of which one alone bears an ovule, or whether 'condensation' has reached a point at which only one of the two can be considered as surviving. The same problem arises in the Chenopodiaceæ (see under that Family later in the present Volume, Part 10, p. 360).



## 105. BETULACEÆ

Inflorescence a catkin. The full scheme of the catkin consists of a racemose series of 3-flowered cymes accompanied by bracts as shown in Fig. 12, but in many types the cymose units are incomplete through suppression of some of the bracts or of the median flower or of the lateral pair.

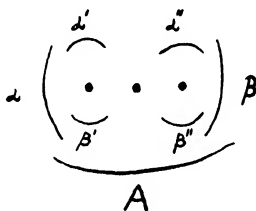


Diagram of the complete cymose unit of the catkin.

A, bract.  $\alpha$ ,  $\beta$ , primary bracteoles.  $\alpha'$ ,  $\beta'$ ,  $\alpha''$ ,  $\beta''$ , secondary bracteoles.

FIGURE 12.

Flowers unisexual, in different catkins, monœcious. Perianth absent or represented by very rudimentary structures. ♂ Cyme more or less adnate to the subtending bract. ♂ Flower. Stamens in flowers with tepals superposed upon them, often duplicated; each resulting pair generally with the filaments conjoined for a longer or shorter distance. ♀ Cyme free from the subtending bract. ♀ Flower. G 4, 2 sterile, 2 fertile. Ovary generally bilocular at the base becoming unilocular above as the fertile carpels come to an end. Styles 2, distinct or united at the base, standing over the sterile carpels, stigmatic along their length. Ovules 2, pendulous, only reaching development after pollination. Fruit one-seeded, indehiscent.

In the duplicated stamens of the ♂ flower the common portion of the filament has only a single vascular bundle

which forks as the filament divides in two. The vascular system of the gynæceum consists of four bundles corresponding with the four carpels. Those of the sterile pair are already differentiated at the time of flowering, those of the fertile pair not till some time after pollination.

## ILLUSTRATIVE TYPES

\***Betula alba** (Birch). ♂ Cyme 3-flowered. ♂ Flower. A 2, duplicated, the filaments of each resulting pair joined nearly to the top. ♀ Cyme 3-flowered. ♀ Flower G 4, 2 sterile, 2 fertile.

\***Alnus glutinosa** (Alder). ♂ Cyme 3-flowered. ♂ Flower. A 4. ♀ Cyme 2-flowered, the median flower being suppressed. ♀ Flower. G as in *Betula* (see above).

\***Corylus Avellana** (Hazel). ♂ Cyme 1-flowered. ♂ Flower. A 4 duplicated, the filaments of each pair becoming free at some distance from the top. ♀ Cyme 2-flowered. ♀ Flower. G as in *Betula* (see above).

\***Carpinus Betulus** (Hornbeam). ♂ Cyme probably 3-flowered, but the number uncertain owing to the absence of bracteoles and perianth structures which ordinarily serve to indicate the limits of the individual flower. ♂ Flower. A (probably) generally 4, duplicated. ♀ Cyme 2-flowered. ♀ Flower. G as in *Betula* (see above).

## 106. FAGACEÆ (CUPULIFERÆ)

Flowers almost always unisexual and in separate inflorescences, the ♂ often catkin-like, monœcious. Mixed inflorescences with ♀ flowers exceptional. ♂ Flowers borne on the 'catkin' axis in 3-7-flowered dichasial groups; ♀ flowers borne singly or in 3-flowered groups, rarely in 4-7-flowered groups; the single flower or group wholly or partly enclosed in a cupule formed of four conjoined secondary bracteoles ( $\alpha'$ ,  $\beta'$ ,  $\alpha''$ ,  $\beta''$ ). (For the bract complement of the fully developed dichasium in a typical catkin see under Betulaceæ earlier in the present Volume, Part 9, p. 330, Fig. 12.) Perianth more or less gamophyllous. Tepals bract-like, 4-8, generally 6 in two trimerous whorls. ♂ Flower. A 6-12,  $\pm$  G rudiment. ♀ Flower syngonous, rarely with staminodes. G 3-6 (or more), sterile + 3-6 (or more), fertile with 3-6 (or more) styles or stylar arms. Fruit one-seeded, indehiscent.

## ILLUSTRATIVE TYPES

**Castanea vulgaris** (Sweet Chestnut). ♂ Catkin erect, with numerous 3-7-flowered dichasial groups. ♂ Flower. T generally 3 + 3, sometimes 5, 7 or 8 A 8-12 G a mere rudiment. ♀ Inflorescence erect, with numerous 3-flowered, rarely 4-7-flowered dichasial groups; each group completely enclosed except for the styles in a cupule of four bracteoles which split apart when the fruits ripen. ♀ Flower. Tepals as in the ♂ flower,  $\pm$  staminodes with rudimentary anthers, superposed upon, and also alternating with, the tepals, G generally 6 (or more), sterile + 6 (or more), fertile, but the fertile sometimes, owing to crowding, only reaching development as incomplete partitions at the level at which those forming complete partitions have ceased to develop ovules.

Ovary generally 6-locular, becoming unilocular above as the fertile carpels become gradually withdrawn from the centre into the ovary wall. Styles stiff, acicular, as many as the sterile carpels and superposed upon these carpels. Stigmas terminal, punctiform.

Mixed inflorescences occur occasionally on the stronger shoots, the lower groups being ♀, those following hermaprodite-polygamous, and the uppermost ♂.

In the ♀ flower the vascular cylinder enlarges at the flower base forming a ring of bundles at the periphery and leaving behind a central core representing the fused placental bundles of the fertile carpels. In the ovule-bearing region this central core becomes resolved into its component placental bundles. Towards the summit of the ovary the bundles of the peripheral ring break up to give rise to the tepal midribs, staminode bundles and the midrib bundles of the carpels. As the ovary becomes unilocular and the fertile carpels (septa) become withdrawn from the centre and thus free on their inner face, these carpels undergo median radial splitting from within outwards so that as the ovary gives place to the several styles each style, as it takes shape, receives the midrib of a sterile carpel and half the vascular system of the fertile carpel on each side, and hence represents  $\frac{1}{2} \times 1 \frac{1}{2}$  carpels. (See p. 152.)

**\*Fagus sylvaticus** (Beech). ♂ Inflorescence of pendulous, stalked, many flowered glomerules. ♂ Flower. T 4-7 A 7-12 G an undifferentiated rudiment. Stamens when isomerous with the tepals standing in front of them, when more numerous also alternating with them. ♀ Inflorescence erect, of one 2-flowered group (= a dichasium lacking the central flower), enclosed in a cupule splitting later into the four component bracteoles as in *Castanea* (see above). ♀ Flower. T 3 + 3 G 3, sterile + 3, fertile. Ovary trilocular. Styles distinct, centred over the sterile carpels, channelled and stigmatic on their inner face.

**\*Quercus** (Oak). ♂ Inflorescence pendulous, with numerous flowers borne singly. ♂ Flower. T 5-7 A 5-12 G 0. Stamens when isomerous with the tepals superposed upon them, when twice as many also alternating with

them. ♀ Inflorescence erect, with 1-5 flowers borne singly. ♀ Flower with the ovary only partially enclosed in the cupule which remains unsplit (acorn cup). T 3 + 3 A o G 3, sterile + 3, fertile. Ovary eventually trilocular, but loculi and ovules only completely formed after pollination. Styler arms with broad stigma lobes centred over the sterile carpels.

## 107. ULMACEÆ

Flowers ♂ or unisexual through abortion, hypogynous. Perianth single. Tepals sepaloid (see 19a and 19b), generally 4 or 5, but sometimes 3 or 6–8, more or less conjoined or wholly free. Stamens as many as the tepals and superposed upon them. Carpels in ♂ and ♀ flowers 4, 2 median sterile, 2 lateral (potentially) fertile. Ovary sometimes bilocular (*Ulmus*) through union of the lateral carpels in the centre, but more often unilocular through failure to develop the second loculus. Styles 2, centred over the sterile carpels, stigmatic down the inner face. Ovule solitary, pendulous from the top of the loculus. Fruit one-seeded and indehiscent, dry and often winged in the median plane (*Ulmus*) or drupaceous (*Celtis*, *Zelkova*).

The vascular bundles for the stamens do not arise independently from the central cylinder, but are carried out conjoined at first with the midrib bundles of the tepals, hence the superposition of these whorls. When the perianth, as in *Holoptelea*, consists of eight or more wholly free tepals, some are often very small and fall early. The stamens superposed upon these minute or missing members then present an illusory appearance of belonging to a second inner whorl alternating with the surviving well-developed tepals.

In types with a laterally compressed gynæceum, in which the median dimension is considerably greater than the lateral, even at the extreme base, the perianth segments standing in the median plane back and front differ correspondingly in size and shape from the others (*Zelkova* spp.).

## ILLUSTRATIVE TYPES

\***Ulmus** spp. (Elm). Tepals 4–8, generally 5, without marginal veins of commissural origin and therefore green (19b, pp. 205 and 208). Stamens equal in number to the tepals and superposed upon them. Carpels 2 median sterile + 2 lateral of which only one is normally fertile. Fruit dry, winged.

## 108. MORACEÆ

Flowers always unisexual, in separate inflorescences, monœcious or diœcious, with, or without a simple perianth. Tepals (when present) free or united, persistent. ♂ Flower. Stamens as many as tepals and superposed upon them. ♀ Flower hypogynous or more or less syngonous. Gynæceum of 2 median carpels, 1 sterile, 1 fertile. Ovary unilocular. Ovule solitary, usually pendulous from near the top of the loculus. Styles 2, often united below, filamentous, stigmatic down the inner face; or sometimes only one present owing to suppression of the one belonging to the hinder (fertile) carpel. Fruit one-seeded, drupaceous or dry, indehiscent, often compound (syncarp or pseudocarp).

The vascular bundles for the stamens do not arise independently, but are carried out from the central cylinder conjoined with the tepal midrib bundles, hence these whorls are superposed.

## ILLUSTRATIVE TYPES

**Morus** (Mulberry). Flowers in catkin-like spikes, monœcious or diœcious. ♂ Flower. T 4, united below A 4 + G rudiment. ♀ Flower hypogynous. T 4 or 3, free, later becoming succulent G 2, one anterior sterile, one posterior fertile. Ovary sessile. Styles 2, equal, or the hinder one shorter or wanting. Fruit a syncarp, the ovary of each flower in the inflorescence enclosed in its succulent perianth, the whole number forming together a compound fructification.

**Ficus Carica** (Fig-tree). Flowers lining the cavity of the pear-shaped flowering axis (fig). ♂ Flower. T 3 united below A 3. ♀ Flower. T 4-6, free G 2, one anterior sterile, one posterior fertile. Style of the fertile carpel as long as that of the sterile carpel, or shorter, or undeveloped. Fruit a pseudocarp.

The vascular system of the gynæceum consists of a dorsal cord which is prolonged into the sterile carpel style, and a ventral cord which is used up in supplying the bundle to the ovule.

**\*Humulus Lupulus** (Hop). ♂ Flower. T 5 A 5.  
♀ Flower partially syngonous. Perianth forming an unsegmented cup enclosing the lower half of the ovary. G 2 as in *Morus* (see above). Fruit dry, indehiscent. Bracts and perianth with numerous glands.



## 109. URTICACEÆ

Flowers generally unisexual through abortion and then monœcious or diœcious, rarely hermaphrodite or polygamous (*Parietaria*), actinomorphic or slightly zygomorphic, hypogynous. Perianth single. Tepals generally 4 or 5; where 4 orthogonal, 2 median outer, 2 inner lateral. ♂ Flower. Stamens equal in number to the tepals and superposed upon them. Gynæceum generally represented by a non-vascular rudiment. ♀ Flower. Stamens generally wholly wanting, rarely represented by staminodes (*e.g. Pilea*). Gynæceum of 2 median carpels, 1 anterior sterile, 1 posterior fertile. Ovary syncarpous, unilocular. Ovule solitary, borne at or near the base. Style single or absent. Stigma extending unilaterally down the style (*e.g. Boehmeria*); or sessile and tufted or brush-like; or of other various forms. Fruit one-seeded and indehiscent, often enclosed in the membranous or fleshy perianth.

Tepals generally with unbranched midribs; always without commissural marginal veins, hence they are green (see Vol. I, Introduction, pp. 9, 10; also 19a, 19b). In the ♂ flower the stamen bundles are carried out from the central cylinder conjoined with the tepal midrib bundles, hence the two whorls are superposed. In the ♀ flower the considerable number of vascular elements remaining after the tepal bundles have turned outwards become consolidated into two opposite bundles, one becomes the sterile carpel midrib and may be prolonged into the style, one stouter, serves the fertile carpel and comes to an end at the level of origin of the ovule.

## ILLUSTRATIVE TYPES

\**Urtica* (Stinging Nettle) (19b, p. 207). Flowers unisexual, monœcious in *U. urens*, diœcious in *U. dioica*. ♂ Flower. T 4 A 4 G rudimentary. ♀ Flower. T 4 A 0 G 2. Stigma sessile, tufted.

\**Parietaria officinalis* (Wall Pellitory) (19b, p. 207). Flowers polygamous. ♂ and ♀ Flowers with style bearing a mop-shaped, brush-like stigma.

## 110. PROTEACEÆ

Inflorescence a raceme, spike, head or umbel. Flowers one or two together in the axils of deciduous or hard and persistent bracts, ♂ or rarely through abortion unisexual, polygamous or diœcious, hypogynous, generally actinomorphic seldom zygomorphic. Perianth single, petaloid. Tepals 4, diagonal, occupying the angles of the 4-sided outline, valvate, generally separating from one another and becoming reflexed after the flower unfolds. A 4 or fewer by suppression, antetepalous G 2, one valve sterile, one consolidated fertile. Ovary sometimes central within a ring of four disc structures alternating with the tepals, more often excentric through the presence of a unilateral disc; sessile or with a longer or shorter stipe, unilocular. Style single, derived from both carpels, often, owing to elongation of the lower portion and of the ovary stipe, protruding between the tepals like a bow with the end, which is often enlarged, held fast within the ring of anthers and tepal tips. Stigma small, terminal. Ovules several in two rows, or 2, or solitary. Fruit sometimes folliculoid, dehiscent down the ventral mid-line or in the mid-line of both carpels; sometimes nut-like or drupaceous and indehiscent.

The tepals with commissural marginal veins, hence their petaloid colouring (see Vol. I, Introduction, pp. 9, 10; also 19a, 19b). The vascular bundles for the stamens are carried out conjoined with the tepal midrib bundles, hence the superposition of these whorls.

Above the level of origin of the single ovule or (if more than one) of the lowest pair of ovules, the loculus is continuous with the exterior through an opening in the ventral mid-line of the ovary wall between the twin fertile bundles of the consolidated fertile carpel, such as occurs in similar dimerous

ovaries in other Families, *e.g.* Leguminosæ (see under that Family earlier in the present Volume, Part 5, p. 184).

### ILLUSTRATIVE TYPES

**Grevillea spp.** (19*b*, pp. 206–208, with Fig. 10A–H).  
See the characters of the Family.

## III. SANTALACEÆ

Chlorophyll-containing parasites growing on the branches or the roots of other plants. Flowers ♂, or through abortion polygamous or unisexual and then monœcious or diœcious, more or less syngonous, actinomorphic. Perianth single. Tepals sepaloid or petaloid, generally 4 or 5, united below. Stamens as many as tepals and superposed upon them. Carpels in two whorls; when isomerous with the tepals the outer, sterile carpels alternate with the tepals in ♂ types, superposed upon the tepals in ♀ forms. Ovary multilocular or unilocular according as the fertile carpels extend from the outer wall to the centre or merely form a central column. Style single with capitate stigma or stigma almost sessile. A well-developed lobed disc with the lobes alternating with the stamens sometimes present lining the bottom of the perianth tube. Ovules pendulous from a central column, 3, 4 or 5 according to the number of fertile carpels present, one ovule being formed in each loculus or bay. Fruit one-seeded, indehiscent, nut-like or drupaceous.

Tepals with commissural marginal veins and then variously coloured (purple, lilac, white, greenish yellow) or without such veins and then green (see Vol. I, Introduction, pp. 9, 10; also 19*a*, 19*b*).

In the ♂ flower the vascular bundles for the stamens do not originate independently, but are at first carried upwards conjoined with the tepal midribs from which they are detached, usually after exsertion of the perianth. In the ♀ flower the sterile carpel midribs are similarly conjoined at first with the tepal midribs, but are usually detached from them near the base of the ovary. In the ♂ flower the stamen bundles are detached, as in the ♂ flower, from the tepal midribs, and the sterile carpel bundles in isomerous types, similarly, from the tepal commissural veins. Hence it follows that in isomerous ♂ flowers the sterile carpels alternate with, and in ♀ flowers are superposed upon, the tepals. In flowers with a trimerous

gynæceum two sterile carpel midribs are derived from tepal midribs and one from a tepal commissural vein, approximately equal spacing being thus secured. The vascular system of the fertile carpels is derived from residual strands which become 'condensed' at the base of the ovary into a solid core.

## ILLUSTRATIVE TYPES

**Colpoon** (19b, p. 208). Flower ♂, isomerous throughout, pentamerous or tetramerous. G 5, sterile + 5, fertile or 4, sterile + 4, fertile. Ovary with 5 or 4 loculi below, becoming unilocular above.

Tepals with commissural marginal veins. Sterile carpels with midrib bundles which are detached from the cords which also furnish the commissural marginal bundles of the tepals.

**Osyris** (19b, p. 208). Flowers unisexual, tetramerous throughout. G 4, sterile + 4, fertile. Ovary quadrilocular.

Tepals without marginal veins. Sterile carpels with midrib bundles which are detached from the cords which also furnish the midrib bundles of the tepals.

**\*Thesium** (19b, p. 208). Flowers ♀ with an oligomerous gynæceum. T 5 A 5 G 3, sterile + 3, fertile. Ovary unilocular.

Tepals with commissural marginal veins. In the free tepal segments these veins run their course so near to the midribs as to simulate veins of true lateral origin. (For the converse case, in which true lateral veins present an illusory appearance of commissural origin, see later in the present Volume under *Asperula* in Rubiaceæ, Part 13, p. 474). Sterile carpels with, or without well differentiated midrib bundles; where these bundles are present one is detached from a tepal midrib bundle and two from tepal commissural veins.

**T. capitatum**. Sterile carpels with well differentiated midrib bundles.

**\*T. linophyllum** (**T. humifusum**) (Bastard Toadflax). Sterile carpels without differentiated midrib bundles.

## 112. LORANTHACEÆ

Plants with chlorophyll but generally parasitic and growing on the branches of other plants. Flowers ♂ or unisexual and then monœcious or diœcious, generally actinomorphic, rarely slightly zygomorphic, syngonous, the ovary wholly sunk in the concave end of the floral axis, or the axial cup with an entire or toothed edge extending only part way up the ovary, forming a distinct rim (calyculus). Tepals 4, 5, 6 or 8, sometimes petaloid (see below). Stamens isomerous with the tepals and superposed upon them. Gynæceum with little morphological differentiation. In types with a single perianth (*e.g.* T 5) sterile carpels isomerous with the tepals and alternating with them. In types with a perianth of two whorls (T 3 + 3) sterile carpels isomerous with the inner whorl. Fertile carpels isomerous with the sterile carpels, united into a central column without differentiation of placentæ or ovules. Style single with capitate stigma or stigma(s) sessile. Fruit consisting of axis + gynæceum, baccate or drupaceous.

Tepals with unbranched midribs or with one or two true lateral veins (19*b*, p. 208). In forms with coloured tepals, such *e.g.* as *Loranthus*, the colouring is not confined to the tepals, but is general, and hence without direct relation to the vascular scheme (*loc. cit.*, p. 209). The vascular bundles for the stamens do not arise independently but are conjoined, at first or completely, with the tepal midribs, hence these whorls are superposed.

## ILLUSTRATIVE TYPES

## (i) LORANTHOIDEÆ

Plants generally, but not always, parasitic. Calyculus present. Flowers ♂ or unisexual. Tepals often large and coloured.

**Loranthus europæus.** Parasitic mainly on *Quercus* (Oak) and *Castanea* (Sweet Chestnut). Flowers unisexual, with rudiments of the non-functional sex, diœcious. ♂ Flower. T 6 A 6 G rudimentary. ♀ Flower. T 6 A 6 rudimentary G 3, sterile + 3, fertile. Fruit baccate.

The vascular bundles of the stamens are detached from the trunk cords which also furnish the tepal midribs.

## (ii) VISCOIDEÆ

Plants always parasitic. No distinct calyculus. Flowers always unisexual, monœcious or diœcious.

\***Viscum album** (Mistletoe). Parasitic on many trees, particularly on *Pirus Malus* (Apple) and *Populus* (Poplar). Flowers diœcious, ♂ generally, ♀ always, without rudiments of the non-functional sex. ♂ Flower generally T 4 A 4 (when terminal T 6 A 6). Anthers sessile, conjoined along the dorsal face with the tepals, opening by numerous pores. ♀ Flower generally T 4 G 4, 2 sterile, 2 fertile, sometimes T 3 G 3, sterile + 3, fertile. Stigma sessile. Fruit baccate.

The vascular system of the ♂ flower is more 'condensed' than in *Loranthus* (see above). No separate staminal component is detached from the single cord on each tepal radius which passes entire into the exerted tepal as the midrib. In the ♀ flower the vascular system of the gynœceum only becomes well differentiated after pollination. But in the early fruiting stages the sterile carpel midribs are readily observed in transverse section turning outwards from the centre. The vascular complex remaining behind on each alternate radius represents the system of a fertile carpel.

## 113. ARISTOLOCHIACEÆ

Flower ♂, syngonous, actinomorphic or zygomorphic. Perianth single (*e.g.* *Aristolochia*, *Asarum spp.*) or rarely double (sometimes in *Asarum europæum* and *A. canadense*), the members of the inner whorl when present being reduced to small non-vascular teeth. Whether single or double, coloured, for commissural marginal veins are present in both tepals and sepals and the sepals, like the tepals which they resemble, owing to the absence of vascular elements in the petal rudiments, receive the whole perianth component of the vascular cords turning outwards on the petal radii (see Vol. I, Introduction, pp. 9, 10; also 19*b*, p. 208). A parallel case to that of the two above-mentioned species of *Asarum* occurs in the sterculiaceous genus *Thomasia* in which an outer perianth whorl, the members of which have commissural marginal veins, is coloured (or white) notwithstanding the presence of an inner perianth whorl in the form of minute glandular structures on the alternate radii; for these structures are without vascular tissue (see under Sterculiaceæ in Vol. I, Part 4, p. 118; also 15, pp. 104–106, with Fig. 43, and 19*b*, p. 204, Fig. 9). Floral ground-plan (generally) T 3 (or K 3 C 3) A 6 + 6 and filaments free or 6 + 0 with the filaments fused with the style column (gynostemium) and then either equally spaced or approximated in three pairs G 6, sterile + 6, fertile. Ovary with 6 loculi, sometimes becoming unilocular above as the fertile carpels fail to reach the centre. Style single. Stigmas 6, either all distinct and centred sometimes over the sterile carpels, sometimes over the fertile carpels ('commissural'); or fused in pairs, the three resulting compound stigmas then being centred over alternate sterile carpels. Ovules generally in two rows in each loculus. Fruit a capsule, in *Aristolochia* dehiscing septicidally through radial splitting of



the fertile carpels (septa) or loculicidally and septifragally, in *Asarum* somewhat irregularly.

The change from a trimerous arrangement in the perianth to hexamerous whorls in the andrœcium and gynœceum is limited to the floral ground-plan, the vascular scheme being based on a hexamerous ground-plan for the perianth as well as for the inner whorls (see below under *Aristolochia* among Illustrative Types).

## ILLUSTRATIVE TYPES

**\**Asarum europæum*.** T 3 (or K 3 C 3). A 6 + 6, distinct G 6, sterile + 6, fertile. Flower actinomorphic, syngonous. Tepals free above. Ovary with 6 loculi throughout. Stigmas 6, centred over the sterile carpels.

***Aristolochia* (Birthwort).** (Generally) T 3 A 6 + 0, united with the style column (gynostemium). Filaments then equally spaced (e.g. *A. Clematitis*, *A. Pistolochia*, *A. rotunda*) or approximated in three pairs (e.g. *A. Sipho*, Dutchman's Pipe). G 6, sterile + 6, fertile. Flower zygomorphic, syngonous. Tepals united throughout. Anthers almost sessile, the very short filaments dividing in two as they separate from the style column; there is

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FIG. 13 A-E. *Asarum caudatum*. Transverse sections of the flower taken at successively higher levels. A. The flower base. Within the endoderms are an outer ring of six trunk-cords on one set of radii which serve the tepals, outer whorl of stamens and sterile carpels; and an inner ring of six cords on the alternate radii which become the placental bundles of the fertile carpels. B. The flower at the level at which the six trunk cords of the outer ring turn horizontally outwards preparatory to the appearance of the loculi. C. The same after the formation of the six loculi. Lateral bundles given off on each side of the trunk cords have met on the intervening (alternate) radii and from these meeting points six reconstructed bundles have arisen which become the bundles of the six inner stamens. D. The same above the level of exertion of the perianth (not represented) and outer whorl of stamens. In line with the exerted outer staminal whorl the sterile carpel midrib bundles which are divided in two and the loculi. On the alternate radii the bundles for the inner ring of stamens and the pairs of placental bundles of the fertile carpels. These carpels have now become defined on their inner face, but still remain in contact. E. The gynœceum above the level of exertion of the perianth and andrœcium. In line with the six sterile carpels the six stigma brushies. The loculi have closed after becoming continuous with the styler canal by the channels (indicated by radial lines) formed as the fertile carpels separate on their inner face. The fertile carpels have also begun to split in the middle line from the centre outwards, hence the scalloped outline of the canal.

*a 1* vascular bundle of a stamen of the outer whorl. *a 2* vascular bundle of a stamen of the inner whorl. *e* endodermis. *g 1* sterile carpel midrib bundle. *g 2* placental bundles of the fertile carpels. *ts* initial split of the fertile carpels. *l* loculus. *rb* reconstructed bundle. *sc* styler canal. *sp* stigmatic papillae. *tc* trunk cord.

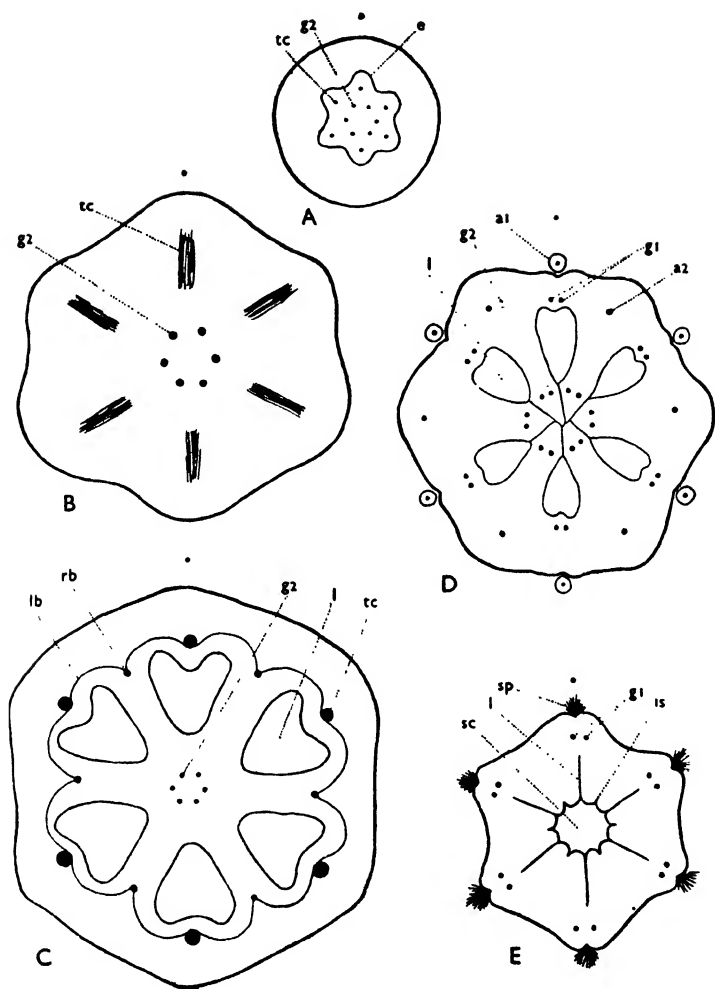


FIGURE 13 A-E.

thus no connective, the two thecae of each anther being quite separate. Ovary with 6 loculi at the base, becoming almost at once unilocular as the fertile carpels cease to reach the centre. Stigmas either 6, distinct, equally spaced and centred over the fertile carpels ('commissural') (as in *A. Clematitis*, *A. Pistolochia*, *A. rotunda*) or 3, through fusion in pairs, being then centred over alternate sterile carpels (as in *A. Siphon*).

The vascular scheme of both the above genera is based on a hexamerous ground-plan, but differs in detail in accord with the differences in the floral ground-plan described above.

In *Asarum* (Fig. 13 A-E) the whole vascular system consists at the flower base of *two* alternating rings of six cords, the cords of the outer ring standing on the radii of the loculi, those of the inner ring on the alternate radii (Fig. 13 A). These latter cords become organised directly into the placental bundles of the six fertile carpels. As the flower base enlarges the six trunk cords of the outer ring turn outwards (Fig. 13 B). From each of these cords a lateral branch is given off on each side (Fig. 13 C). The adjacent branches of neighbouring cords meet mid-way and uniting give rise to six new bundles standing in line with the septa (fertile carpels) (Fig. 13 C). In the upper region of the ovary the six cords in line with the loculi

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FIG. 14 A and C-F. *Aristolochia Clematidis*. B. *A. Pistolochia*. All from transverse sections of the flower taken, when in series, at successively higher levels. A. The flower base showing a single ring of six trunk cords and in the centre a solid core of undifferentiated vascular elements which at a higher level become organised into the placental bundles of the six fertile carpels. B. The flower after the appearance of the loculi in line with the primary trunk cords. In the centre the placental bundles of the six fertile carpels on the alternate radii. C. The same after the ovary has become unilocular through the withdrawal of the fertile carpels from the centre. [For the sake of simplicity only the ovules borne by one of these carpels have been represented.] Short lateral branches have been formed by the primary trunk cords, but they do not reach to the alternate radii and do not therefore give rise to a new trunk cord as in *Asarum* (see Fig. 13 C). D. The same at the level at which the six primary trunk cords again give off a pair of lateral branches and then turn outwards horizontally. Three of these horizontal bundles become the midrib bundles of three tepals, the alternate three furnish commissural marginal veins. E. The same after the exertion of the perianth (seen as a separate outer ring with three midrib bundles and three commissural marginal veins). In the centre the still united androecium of six alternitepalous stamens and style column with styler canal. In line with each stamen a secondary trunk cord arising from the meeting point of the lateral branches of the primary trunk cords seen in D. These reconstructed cords break up into twin out-turning strands for the two halves (thecae) of each anther and a residual central strand (= a fertile carpel midrib which only comes into separate being at this level) which ends beneath the corresponding 'commissural' stigma. F. The six 'commissural' stigmas superposed upon the six residual central vascular strands seen in E, which have now come to an end. *a* stamen vascular bundle. *cm* commissural marginal veins. *g* 2 placental bundles of the fertile carpels. *l* loculus. *lb* lateral branch. *sc* styler canal. *sg* stigma bundle. *tc* trunk cord. *tm* tepal midrib.

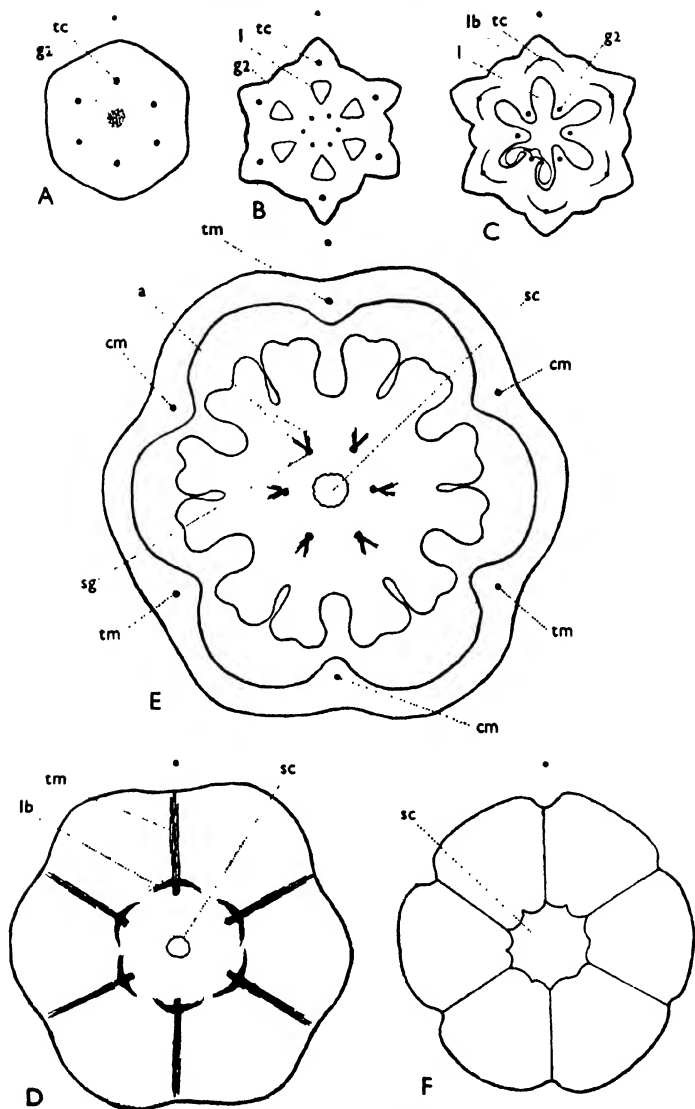


FIGURE 14 A-F.

break up into (a) the three midrib and three commissural bundles of the perianth, (b) the six bundles for the outer stamen whorl, (c) the six pairs of twin strands representing the sterile carpel midribs (Fig. 13 D). The six reconstructed bundles on the alternate radii pass direct into the stamens of the inner whorl. The sterile carpel midribs continue upwards into the style column and the stigma lobes are centred over them (Fig. 13 E).

In *Aristolochia Clematidis* and similar species (Fig. 14 A-F) the vascular system at the flower base consists of a single ring of six cords, from which portions are at once detached and turn inwards to form a solid central core (Fig. 14 A) which becomes organised at a higher level into the placental bundles of the six fertile carpels (Fig. 14 B). After these portions have been detached the six original cords continue upwards in line with the loculi. But although, as in *Asarum* (see above), a lateral branch is given off on each side by each of these cords (Fig. 14 C), no new main bundles are reconstructed at junction points at this level as in *Asarum*. Since in *Aristolochia* no inner stamen whorl is present. At the top of the ovary these six cords turn outwards to become the three midribs and three commissural bundles of the gamophyllous perianth (Fig. 14 D). The three midrib bundles continue as far as the edges of the flat limb of the perianth. Of the three commissural bundles two come to an end before reaching the edge of the limb. Only the third forks in the typical manner of the commissural bundle and provides a marginal vein to right and left on the anterior lip as the tube opens out. In their course outwards each of the above-mentioned six cords leaves behind a residual portion. These residual portions give off a lateral branch on each side (Fig. 14 D). From the meeting and union of these branches mid-way between the parent bundles a new set of six bundles arises on the alternate radii. In some species in which the very short split filaments of the stamens are without independent vascular tissue these new reconstructed bundles remain intact and serve the six 'commissural' stigmas. In other species the central portion of each of these bundles serves the corresponding stigma, the two lateral portions the twin filaments of each split staminal member (Fig. 14 E).

## Part 10

### Dicotyledons

Family	114.	Polygonaceæ
„	115.	Chenopodiaceæ
„	116.	Amarantaceæ
„	117.	Nyctaginaceæ
„	118.	Phytolaccaceæ
„	119.	Aizoaceæ
„	120.	Basellaceæ
„	121.	Ceratophyllaceæ
„	122.	Trochodendraceæ
„	123.	Anonaceæ
„	124.	Monimiaceæ
„	125.	Calycanthaceæ
„	126.	Lauraceæ



## 114. POLYGONACEÆ

Flowers ♂ or unisexual, hypogynous, cyclic or hemi-cyclic; either with a perianth of two usually dissimilar whorls and then generally isomalous throughout with trimerous or dimerous whorls; or with a single pentamerous perianth of similar members and a tri- or dimerous gynæceum. In isomalous cyclic types with two staminal whorls the outer whorl is frequently duplicated, the inner whorl sometimes suppressed. In heteromalous types with a single perianth the stamens are sometimes in two whorls, sometimes in one whorl. When in two whorls duplication may occur, as in isomalous types, but neither whorl is generally complete; when in one whorl this whorl is generally complete and alternates with the perianth segments. Scale-like or glandular (disc) structures often present between the andrœcium and gynæceum (*e.g. Rheum*) or between the stamens (*e.g. Polygonum*). The gynæceum consists of three tri- or sometimes dimerous whorls, the two outer whorls forming the wall of the ovary, the third inner whorl forming a central column from which, as it comes to an end, springs a single ovule. The formation of three carpel whorls is rare. It occurs also in Balsaminaceæ (see under that Family in Vol. I, Part 3, p. 81). Ovary always unilocular. Ovule always solitary, basal, almost always orthotropous. Styles separate or conjoined for a longer or shorter distance, centred over the outer whorl of sterile carpels. Stigmas capitate. Fruit one-seeded indehiscent.

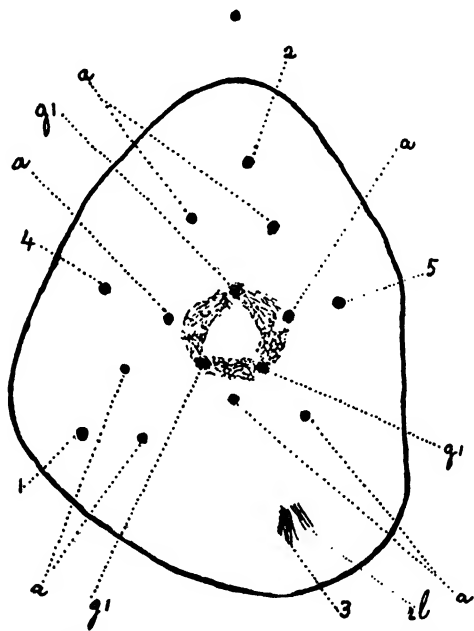
In some forms with a single perianth the tepals have true lateral veins and are therefore green (*e.g. Muehlenbeckia*); in others the tepals have commissural marginal veins and are coloured, but the direct connection between this coloration and the vascular scheme is masked by



general 'flooding' of the region of the inflorescence with colour (*e.g. Polygonum*) (see Vol. I, Introduction, pp. 9, 10; also 19*b*, p. 204, Fig. 6, and pp. 208, 209). The vascular bundles for the stamens turn out from the central cylinder independently. In isomerous trimerous types (*e.g. Rheum, Rumex*) duplication of the outer staminal whorl is associated with the three-angled form of the ovary. The midrib bundle of each outer perianth member and those of the superposed pair of stamens are derived from the same vascular unit. This unit has already become defined at the level at which the perianth bundles turn outwards from the centre (well seen in *Rumex vesicaria*), hence the two stamens of each pair are whole stamens. The turning outwards of the sterile carpel bundles, which occupy the angles of the ovary, causes the staminal vascular units left behind by the outgoing outer perianth bundles to become divided in two and leads to duplication of the corresponding staminal members. Similar duplication of a staminal whorl is associated with the angled outline of the gynæceum in *Monsonia* and *Sarcocaulon* among Geraniaceæ (see under this Family in Vol. I, Part 3, pp. 69 and 72, also 16, p. 102, Figs. 91-95). (For the reverse case in which halving of the staminal vascular component corresponding to a single member of the andrœcium is associated with the formation of half stamens (*i.e.* filaments with half anthers) see in Vol. I under Papaveraceæ-Fumarioideæ, Part 2, p. 48, and under Malvaceæ, Part 4, p. 106.)

In types offering favourable material for analysis of the gynæceum (*e.g. Rheum officinale*) the vascular scheme is easily observed to conform to the ground-plan  $G\ 3 + 3 + 3$ . After the bundles for the perianth and andrœcium have turned out from the central cylinder three more bundles leave the centre and become the midrib bundles of the outermost whorl of carpels which occupy the angles of the three-angled three-sided ovary and stand in line with the sepals. These bundles are shortly followed by another set of three out-turning

hemicyclic species is reflected in the vascular scheme of the perianth and of the andrœcium in some A 8 ( $3_1 + 2$ ) species, as e.g. *Polygonum Brunonis* and *Atraphaxis buxifolia*. Ordinarily, in cyclic forms, the pair of primary laterals in a member of the perianth with a pinnate vascular system arise simultaneously, but in *Polygonum Brunonis* the primary laterals in sepal 3 arise successively, the one on the side with an overlapping edge being formed before its fellow on the side with the overlapped edge (see Figs. 15 and 16). Similarly,



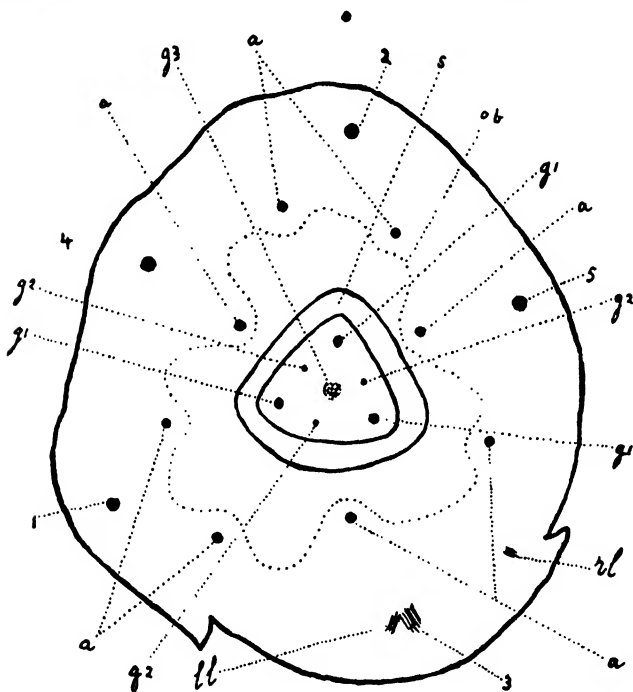
*Polygonum Brunonis*. Type with T 5 A 8 ( $3_1 + 2$ ). Transverse section through the base of the flower.

1, 2, 3, 4, 5 midrib bundles of the quinquecyclically arranged tepals in the order of their development. The midrib bundle of tepal 3 with a lateral branch ( $r l$ ) on the side corresponding with the overlapping edge of the tepal, but not yet on the side corresponding with the overlapped edge.  $a$  stamen bundle. The bundles standing in front of tepals 1, 2 and 3 duplicated, those in front of tepals 4 and 5 single. The pair of bundles in front of tepals 1 and 2 arise simultaneously, and the members of each pair lie equally far from the centre; the pair in front of tepal 3 arise successively, the one in line with the overlapping edge of the tepal developing earlier, and hence standing farther from the centre than the other.  $g_1$  the midrib bundles of the outermost (sterile) carpels in process of being organised. Between these bundles the residual unorganised vascular tissue which gives rise later to the bundles of the second (sterile) and third (fertile) carpel whorls. (Compare Fig. 16.)

FIGURE 15.

in A 8 species such as *Polygonum Brunonis*, the vascular bundles of the two stamens standing in front of tepal 3 do not develop simultaneously, the one in line with the overlapping edge turning outwards before the one in line with the overlapped edge (see Fig. 16).

This delayed development of the latter staminal bundle gives rise to the deceptive appearance that this stamen belongs to the inner whorl and that the arrangement of the



*Polygonum Brunonis*. Type with T 5 A 8 (3, + 2). Transverse section of the flower taken at a higher level than that shown in Fig. 15.

1, 2, 3, 4, 5, a and g<sub>1</sub> as in Fig. 15. g<sub>2</sub> the bundles of the carpels of the second (sterile) whorl. g<sub>3</sub> the residual unorganised vascular tissue which gives rise later to the bundles of the carpels of the third whorl of which only one is fertile. ob outer boundary of the irregular belt of ground tissue lining the flower tube which has become sclerosed. \* space between the flower tube and the gynæceum. The midrib bundle of tepal 3 has begun to form a lateral branch (ll) on the side corresponding with the overlapped edge of the tepal; the lateral branch (2l) formed earlier on the side corresponding with the overlapping edge (compare Fig. 15) has now diverged a considerable distance from the midrib towards the margin of the tepal.

FIGURE 16.

eight stamens is  $A\ 2, 1 + 3$ , whereas, in reality, it is  $A\ 3, + 2$ . In the next stage of reduction to an andrœcium of seven stamens this lagging member of the outer whorl disappears, as e.g. in *Polygonum Bistorta*, *P. aviculare*, *P. orientale*, which have  $A\ 2, 1 + 2$ . Reduction to six stamens as in *P. lapathifolium* and *P. Persicaria* is due to the additional suppression of the stamen occupying the most crowded position, viz. the mid-point in front of tepal 5; consequently these species have  $A\ 2, 1 + 1$ . That this is so is readily observed in a detached corolla. For the basal gland superposed on tepal 4 is bi-lobed owing to the presence of the superposed stamen, but the gland superposed on tepal 5, like those on tepals 1, 2 and 3, is entire since no stamen stands in the mid-line of these tepals. Further reduction to five stamens, as in *P. amphibium*, occurs when the remaining inner stamen which stands in front of tepal 4 is also suppressed. The five surviving stamens then arise as a single whorl alternating with the single whorl of five tepals. The transition from the hemicyclic to the cyclic condition is thus completed.

*Fagopyrum* spp. (e.g. *F. cymosum*) have the same number of floral members as *Polygonum Brunonis* ( $T\ 5\ A\ 8\ G\ 3 + 3 + 3$ , see above), but differ from the last-named species in the ground-plan of the andrœcium. In *Fagopyrum cymosum* the lagging member of the pair of stamens in the outer whorl standing on either side of the mid-line of tepal 3 is replaced by an additional member of the inner whorl standing in the mid-line of tepal 3, so that the whole andrœcium is to be represented as  $A\ 2, 1 + 3$  in place of  $A\ 3, + 2$ .

## ILLUSTRATIVE TYPES

### (i) FLOWER CYCLIC. TEPALS IN TWO WHORLS

**Rheum officinale** (Rhubarb). Flower ♀.  $T\ 3 + 3\ A\ 9\ (3_2 + 3)\ G\ 3 + 3$ , all sterile + 3, (potentially) fertile.

The vascular ground-plan of the gynœceum is particularly easily observed in this species owing to its diagrammatic regularity.

**\*Rumex** (Dock) (19b, p. 202, Fig. 4). Flower ♀.  $T\ 3 + 3\ A\ 6\ (3_2 + 0)\ G\ 3 + 3$ , all sterile + 3, (potentially) fertile.

**Emex spinosa** (19b, p. 202, Fig. 5). Flowers unisexual. ♂ Flower.  $T\ 3 + 3\ A$  (generally) 6 or 5 ( $3_2 + 0$  or  $2, 1 + 0$ ). ♀ Flower.  $T\ 3 + 3\ A\ 0\ G\ 3 + 3$ , all sterile + 3 (potentially) fertile. The inner tepals united below.

The primary lateral veins of each inner tepal anastomose with those of its neighbours thus forming a complete vascular girdle.

(ii) FLOWER HEMICYCLIC. TEPALS IN ONE WHORL, ARRANGED QUINCUNCIALY

**Polygonum Brunonis (affine)** (Figs. 15, 16). Flower ♀, T 5 A 8 ( $3_2 + 2$ ) G 3 + 3, all sterile + 3, (potentially) fertile. The diagrammatic regularity of the vascular ground-plan renders analysis of the andrœcium particularly easy in this species.

**\*P. Bistorta, \*P. aviculare.** Flower ♀. T 5 A 8 (as in *P. Brunonis*, see above) or 7 ( $2_2, 1 + 2$ ) G 3 + 3 (or 2 + 2), all sterile + 3 (or 2), (potentially) fertile.

**\*P. Persicaria, \*P. lapathifolium.** Flower ♀. T 5 A 6 ( $2_2, 1 + 1$ ) G 2 + 2, all sterile + 2, (potentially) fertile.

**P. baldschuanicum.** A species showing considerable variation in the flower under cultivation. T<sub>4</sub> occurs not infrequently owing to the modification of the fifth tepal into a stamen, with the result that on this radius two stamens are superposed, one of them being the modified tepal. G<sub>4</sub> + 4 occurs occasionally through the loss after reconstruction of only one carpel in each whorl instead of the more usual two. Styles and stigmas sometimes reduced to two, even when the vascular ground-plan indicates a trimerous construction, in consequence of the failure of the third sterile carpel to develop beyond the top of the ovary. The presence of a considerable amount of central parenchyma renders this species particularly suitable for observation of the processes of re-organisation and consolidation of the residual vascular elements serving the third carpel whorl.

(iii) FLOWER CYCLIC. TEPALS IN ONE WHORL, ARRANGED QUINCUNCIALY

**\*P. amphibium.** Flower ♀. T 5 A 5 in one whorl, alternating with the tepals and with the five glands which stand in line with the tepals G 2 + 2, all sterile + 2, (potentially) fertile.

## 115. CHENOPODIACEÆ

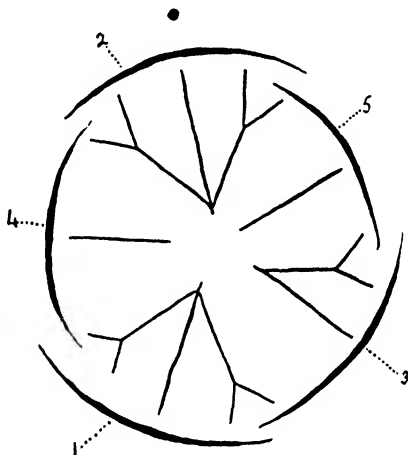
Flowers ♂, polygamous or dioecious, generally actinomorphic, almost always hypogynous. Perianth single, rarely wanting, persistent, sepaloid. Sepals united below, generally 5, sometimes fewer. Stamens as many as the sepals or fewer, always superposed on them, often united below by a glandular ring. Carpels 2-5, sterile + 1 or ? more (see below), but only one fertile. Style (when present) single. Stigmas as many as the sterile carpels and standing over these carpels, generally filamentous, sometimes sessile, broad and flat. Ovary always unilocular. Ovule always solitary, basal, or (exceptionally) borne on the side wall of the ovary (*Beta*). Fruit indehiscent, or eventually opening by a lid.

The sepals have unbranched midribs, or midribs with true lateral veins, but never marginal veins of commissural origin, and are therefore green or hyaline (196, p. 208). Exceptionally, the lowest true lateral veins of neighbouring segments may 'kiss' in the region below the level at which the tepals become free, and in this way give an illusory appearance of being of commissural origin (*e.g. Hablitzia*). (For a similar deceptive appearance due to the same cause, see later in the present Volume under *Asperula* in Rubiaceæ, Part 13, p. 474.) The often feebly-developed vascular bundles of the stamens do not arise independently, but are detached from the inner face of the trunk cords, which also furnish the midrib bundles of the sepals, hence the superposition of the stamens upon these members. Evidence of the number of sterile carpels present in addition to that furnished by the stigmas is afforded in types where they are sufficiently well differentiated by the number of vascular bundles running upwards in the ovary wall (*e.g. Chenopodium Bonus-Henricus, Salsola Kali*). These bundles, like those for the stamens, are detached from the original trunk cords. The consolidation of the residual vascular elements into a solid central core which serves the solitary basal ovule renders it uncertain whether this core represents a single surviving carpel or as many potentially fertile carpels as there are sterile carpels present. The same problem is presented by many other Families in which the vascular system for the fertile carpel whorl is 'condensed' into a central

core (see *e.g.* under Plumbaginaceæ later in the present Volume, Part II, p. 413).

### ILLUSTRATIVE TYPES

**\*Chenopodium spp.** (Goosefoot) Flower ♂, hypogynous. Sepals 5 with unbranched midribs. Stamens 5, with vascular bundles undifferentiated or differentiated only towards the top. G 2, sterile  $\pm$  midrib bundles + (?) 2, one alone being fertile. Stigmas 2.



*Suaeda maritima*. Diagram of the quincuncial calyx with its very unusual vascular scheme.

All five sepals have two marginal veins, but owing to the absence of petals and of antepetalous stamens and consequent absence of vascular bundles on the inter-sepalous radii these marginal veins originate in a different way in the different sepals.

1, 2, 3, 4, 5.—Sepals in order of development. In sepals 1 and 2 both lateral veins arise as true lateral branches from the midrib. In sepal 3 the vein on the side corresponding with the overlapping edge originates in the same way as in sepals 1 and 2; the vein on the side corresponding with the overlapped edge arises, through forking of the adjacent marginal vein of the neighbouring sepal on that side (sepal 1). In sepals 4 and 5 both marginal veins arise through forking of the marginal veins of the adjacent sepal on each side (sepals 1 and 2 and sepals 2 and 3, respectively).

FIGURE 17.

**\*Beta** (Beet). Flower ♂, perigynous. G 3, sterile + (?) 3, one only being fertile. Stigmas 3. Otherwise as in *Chenopodium* (see above).

**\*Suaeda spp.** (*e.g.* **\*S. fruticosa**, **\*S. maritima**) (Fig. 17). Flower ♀, hypogynous. Sepals 5, some with branched midribs

(see below). Stamens 5. Filaments without differentiated vascular bundles, springing from a non-glandular ring-shaped membrane lining the basal region of the perianth. Gynæceum, as in *Beta* (see above), with three stigmas (*S. fruticosa*) or as in most *Chenopodium spp.* (see above) with two stigmas (*S. maritima*).

The unequal conditions set up on the different radii owing to the quincuncial arrangement of the sepals is illustrated in an exceptional manner in the venation scheme of the sepals in *S. maritima*. [For the relations of the members of a whorl thus arranged, see earlier in the present Volume under Saxifragaceæ, Part 5, p. 149, Fig. 7.] In *S. maritima* the midribs of the two wholly outer sepals (1 and 2) develop a pair of basal lateral veins. Those of the two wholly inner sepals (4 and 5) form no basal laterals. The midrib of sepal 3 with one edge outside and one edge inside that of its two neighbours may form a basal lateral on one side only—the side with the edge outside that of the neighbouring sepal (5). Each of these five basal laterals bifurcates, one fork continuing in the sepal in which the lateral originated, the other fork diverging into the neighbouring sepal (see Fig. 17). In this way a uniform vascular system is provided in each sepal, although the manner of origin of the separate systems is not uniform, but follows the scheme of overlapping edges. In some types the unequal conditions obtaining on the radius of the outer edge of sepal 3 or tepal 3 as compared with that of the inner edge in the quincuncially arranged perianth may be reflected in the time of development of the stamens in these positions, as in species of *Polygonum* (see under Polygonaceæ earlier in the present Volume, Part 10, pp. 356, 357, Figs. 15, 16).

**Atriplex** (Orache). Flowers generally unisexual, monœcious or diœcious. ♂ Flower. Sepals 3–5 with unbranched midribs. A 3–5 usually without a differentiated vascular bundle. A rudiment of the gynæceum present. ♀ Flower enclosed in two broad triangular bracts. Sepals wanting A o G 2, sterile + (?) 2, one alone being fertile. Stigmas 2. Sterile carpels without differentiated vascular bundles.

**Spinacia oleraceæ** (Spinach). Flowers ♀, ♂ and ♀. Stigmas 4 or 5.



## 116. AMARANTACEÆ

Flowers ♂, polygamous or unisexual, actinomorphic, hypogynous or partially syngonous. Perianth single, generally pentamerous. Sepals with unbranched midribs or with true lateral veins, or exceptionally, *e.g.* in *Achyranthes argentea*, *Telanthera* (*Alternanthera*) *polygonoides*, *Alternanthera Achyrantha* with marginal veins of commissural origin (see 196, p. 208), A 5 + 5, the inner whorl, except in one genus (*Pleuropetalum*) reduced to non-vascular, antherless staminodes varying from broad scale-like structures to mere teeth, or A 5 + 0 through complete disappearance of the sterile teeth, generally monadelphous for a longer or shorter distance, rarely free to the base, G 2 or 3 (rarely 4), sterile + (?) 2, 3 or 4, only one of which, with rare exceptions (*Pleuropetalum* and some *Celosia spp.*), is fertile. Ovary always unilocular, often surrounded by a glandular ring. Ovule almost always solitary, very rarely few to several (*Celosia spp.*, *Pleuropetalum*), basal. Styles, when present, completely connate or more often separating above into stigmatic branches equal in number to the sterile carpels and centred over these carpels. Stigmas, when sessile, in the form of an apical tuft or brush. Fruit a berry, or dry and indehiscent, or opening by a lid, frequently enclosed by the persistent perianth.

The presence in the perianth segments of some types of lateral veins of commissural origin (see above) affords additional evidence that the inter-staminal scales and teeth are the modified remnants of an inner staminal whorl. For the bundles which bifurcate to furnish these commissural laterals must have originated as components of trunk cords turning out from the centre on these radii. The other component of these cords (since a corolla is wanting) must have been a stamen bundle. As the stamen served by this bundle became sterile the staminal component ceased to develop, but the perianth component persisted. This inference is confirmed by the

evidence from *Pleuropetalum*. In a tetramerous flower of *P. costaricense* all the eight stamens of the monadelphous andræcium bore anthers and possessed a vascular bundle, though the bundles in all remained undifferentiated until near the level of the anthers (unpublished).

Midrib bundles are present in the sterile carpels, but the whole vascular system of the inner carpel whorl, as in Chenopodiaceæ (see earlier in the present Volume under that Family, Part 10, p. 360), is consolidated into a central core, hence the difficulty of determining the number of carpels in this latter whorl.

### ILLUSTRATIVE TYPES

**Amarantus** (Love-lies-bleeding, Prince's-feather).  
Staminodes absent, stamens free to the base.

**Celosia, spp.** (Cock's-comb). Andræcium monadelphous. Staminodes small.

**Gomphrena spp., Achyranthes, Alternanthera spp.**  
Andræcium monadelphous. Staminodes large.

## 117. NYCTAGINACEÆ

Flowers generally invested either singly or in racemose or cymose groups by an involucre of calyx-like or petaloid bracts, ♀, or unisexual but with aborted remains of the non-functional sex, actinomorphic, hypogynous. Perianth single, tubular, funnel- or bell-shaped, generally petaloid, rarely sepaloid; when petaloid with commissural marginal veins (see Vol. I, Introduction, pp. 9, 10; also 19a, 19b), when sepaloid without such veins (*e.g.* *Cryptocarpus*); persisting entire or in part, the upper portion often delimited by a constriction from the basal portion surrounding the ovary, the basal portion often enlarging during the fruiting stage and becoming leathery or woody. Tepals generally 5, seldom 4. Stamens 1-10, in one or two, complete or incomplete whorls, or  $\infty$ , often of unequal length, united at the base into a ring round the ovary. Gynæceum syncarpous of 2 median carpels, one anterior, of valve form and sterile, one posterior, solid and fertile. As the fertile carpel comes to an end the edges of the sterile carpel come together but leave an open pore or channel leading into the loculus before they become fused, as commonly in ovaries of similar construction (see under Leguminosæ and Proteaceæ, earlier in the present Volume, Part 5, p. 184, and Part 9, p. 339, respectively). Style single, formed by the sterile carpel, rarely wanting. Stigma varying in form. Ovule solitary, basal. Fruit enclosed in the persistent portion of the perianth (anthocarp), one-seeded, indehiscent.

The Family affords particularly striking illustrations of the coloration of the single perianth when the marginal veins of the tepals are commissural in origin, the petaloid character being often further enhanced by differences in form and consistency between the median and lateral portions of the tepal segments. In some types owing to

copious branching of the tepal midribs and anastomosis of the midrib and marginal systems the commissural origin of the latter is not obvious in the exerted perianth. But in other forms with a simpler vascular scheme it is easily observed (see below under Illustrative Types).

The vascular bundles for the stamens turn out from the central cylinder independently. When two whorls develop the difference in level of origin of the vascular bundles is inappreciable and the two whorls stand in a single ring. When the stamens are fewer than ten, but not isomerous with the tepals, they are as equally spaced as the ground-plan allows, some members of both whorls being generally present but neither whorl being complete.

### ILLUSTRATIVE TYPES

**Mirabilis Jalapa** (Marvel of Peru) (19b, p. 208). Involucre persistent, of five sepal-like bracts enclosing a single terminal flower. Flower ♂. Perianth petaloid. T 5, with commissural marginal veins, alternating with the 5 bracts of the involucre as with the sepals of an isomerous calyx, A 5 in one whorl alternating with the tepals G 2 with the characters of the Family (see above).

**Oxybaphus spp.** (e.g. **O. glabrifolius**) (19b, p. 208). Involucre persistent, of five bracts enclosing three flowers, one terminal and two axillary. Flower ♀. Perianth petaloid. T 5, showing clearly the commissural origin of the marginal veins A 2 + 1 G 2 with the characters of the Family (see above).

**Borhavia spp.** (e.g. **B. gibbosa**) (19b, p. 208). Involucre of three non-persistent bracts accompanying each flower. Flower ♀. Perianth petaloid. T 5, with commissural marginal veins A 5 + 5 G 2 with the characters of the Family (see above).

**Bougainvillea spp.** (19b, p. 208). Involucre persistent, of three large petaloid bracts adnate, respectively, to the pedicels of the three flowers which they subtend. Flower ♀. Perianth petaloid. T 5, with commissural

marginal veins A 5 + 5 G 2 with the characters of the Family (see above). Stigma linear, extending down the inner face of the tapering style.

**Abronia spp.** (*e.g.* **A. umbellata**) (19*b*, p. 208). Involucre of five persistent bracts. Flower ♂. Perianth petaloid. T 5 showing clearly the commissural origin of the marginal veins, A 5 + 0 G 2 with the characters of the Family (see above).

## 118. PHYTOLACCACEÆ

Flowers ♂ or through suppression in varying degree unisexual, actinomorphic, with one exception (*Agdestis*) hypogynous. Perianth except in two genera (*Limeum* (some species), *Stegnosperma*) single, often coloured (19a, 19b, pp. 205, 208, 210-212). Stamens equal in number to the tepals and in one whorl; or varying up to twice the number through the presence of a complete or incomplete second whorl; or more numerous. Gynæceum completely syncarpous, of two median carpels, one of valve form and sterile, one solid and fertile, forming a unilocular ovary; or syncarpous to near the top of the ovary, of twice as many carpels as tepals or more, forming a multilocular ovary below, but becoming pseudo-apocarpous above; or, through suppression appearing to be completely apocarpous, of about as many carpels as tepals or fewer (14†‡, 18†). Ovules solitary in the loculi. Styles as many as the sterile carpels and centred over these carpels. Fruit when bicarpellary indehiscent, nut-like or a berry; when multicarpellary sometimes berry-like, sometimes separating above into segments of  $\frac{1}{2}$  or  $1\frac{1}{2}$  carpels, sometimes a capsule dehiscing loculicidally.

The Family includes many genera illustrating the relation existing between the vascular scheme and the development of colour in the single perianth (see below under Illustrative Types).

A characteristic of those types in the Family having a multicarpellary syncarpous gynæceum is the very unusual one that it is the outer carpel whorl which is fertile and the inner which is sterile, a rare arrangement but occurring as a Family characteristic also in Geraniaceæ (see under that Family in Vol. I, Part 3, p. 70). In some of these phytolaccaceous types the inner carpels have lost all vascular tissue. The construction of the ovary from two

carpel whorls is then not at once obvious, the surviving vascular ground-plan being in accord with the presence of only a single whorl of carpels, all of the valve type and fertile. This appearance led earlier to the adoption of this latter interpretation for the species of *Phytolacca* examined (see 14, pp. 82-84†), which have then to be regarded as furnishing a solitary exception to the general character of valve carpels which in other hypogynous types when present alone are truly apocarpous. The evidence that the fertile carpels in *Phytolacca* are as described of the valve type is clear beyond question. But in some more recently examined gynæcea of the species originally investigated and described (see 14, *loc. cit.*) groups of undifferentiated vascular elements were observed at the extreme base of the gynæceum on the radii alternating with the valve carpel midribs (*i.e.* the radii of the septa). It then became evident that these partitions are not formed of the fused sides of adjacent valve carpels but are formed of the whole carpels of an alternate whorl which have almost completely lost their vascular tissue (unpublished). This construction is found to be in accord with the appearance at the summit of the ovary where the central parenchyma of the axis comes to an end. At this level these sterile inner carpels, now free on their inner face, begin to split radially from within outwards in the manner frequently seen in consolidated carpels under similar conditions. As this splitting becomes complete the ovary in its upper region becomes pseudo-apocarpous, each partially separate portion being formed of a whole fertile valve carpel flanked on each side by half a sterile carpel ( $\frac{1}{2}$  +  $\frac{1}{2}$ ). This new evidence makes it clear that the multicarpellary syncarpous *Phytolacca* gynæceum is not of unique construction but accords with that of the other multicarpellary syncarpous types in the Family (see further under Illustrative Types). In the

apparently wholly apocarpous few-carpelled species these undifferentiated vascular strands of an inner sterile carpel whorl alternating with the differentiated bundles of the outer fertile carpels have disappeared. The gynæceum in these types consists of a few wholly disjoint ovaries alternating with, and separated by, processes of the surrounding ring of disc tissue which project between them. If the non-vascular as well as the vascular tissue of the sterile carpels is to be looked upon as having been lost, the resulting condition of secondary apocarpy becomes outwardly indistinguishable from the primary apocarpy, characterising in particular those Families or types which have retained the acyclic arrangement and with it the single type of carpel.

## ILLUSTRATIVE TYPES

### RIVINÆ

Flower ♀. Ovary bicarpellary.

**Rivina humilis** (14, pp. 90, 92, 93, with Figs. 20-24 and p. 94, Diagram B; 18, pp. 180-182, with Figs. 5, 6; 21, pp. 66, 67). Flower tetramerous. T 4, in two pairs, orthogonal, with petaloid margins, A 4, diagonal G 2, median, syncarpous, the anterior carpel of valve form, sterile, the posterior solid and fertile (14, *loc. cit.*). The fertile carpel comes to an end at the level of origin of the solitary basal ovule. The meeting edges of the sterile carpel close over the end of the fertile carpel, leaving an open pore into the loculus before they become completely fused, a feature characteristic of bicarpellary ovaries in other Families (see earlier in the present Volume under Leguminosæ, Part 5, p. 184; Proteaceæ, Part 9, p. 339; Nyctaginaceæ, Part 10, p. 365). Style single. Stigma terminal. Fruit a berry.

The bract subtending each flower is exserted at the base of the pedicel, the two bracteoles at the summit, immediately



beneath the flower. Both the bract and the pair of bracteoles lack a vascular bundle. Nevertheless the tepal vascular ground-plan is unusual in that the formation of the midrib bundle for the posterior tepal is delayed. Instead of turning out from the central cylinder simultaneously with that for the anterior tepal and before those for the lateral tepals, it follows after these latter bundles (18, *loc. cit.*). Whereas, ordinarily, in tetramerous types in which the tepals (or sepals) are in two pairs, the bundles for the members of each pair arise simultaneously.

Tepals with commissural marginal veins, hence the white or coloured (non-green) borders of these members (see Vol. I, Introduction, p. 10, and under Sterculiaceæ, Part 4, p. 114; also 18, *loc. cit.*, and 19b, pp. 208, 212; and in the present Volume under Cephalotaceæ and *Chrysosplenium* among Saxifragaceæ, Part 5, pp. 142 and 156, respectively; under Polygalaceæ, Part 6, p. 205; under Thymelæaceæ, Part 7, p. 265; and under Combretaceæ, Part 8, p. 284).

**Ledenbergia roseo-ænea** (14, pp. 89-91, with Figs. 13-15; 18, pp. 180-182, with Fig. 7; 19b, pp. 208, 212). T 4, orthogonal, coloured A 4<sub>2</sub>, diagonal + 4, orthogonal G 2, median. Ovary and style as in *Rivina humilis* (see above). Fruit dry, indehiscent.

The character of the bract and bracteoles and the order of development of the tepal midrib bundles as in *Rivina humilis* (see above). Tepals with commissural marginal veins. The relation between the radius of origin of the marginal veins and the occurrence of petaloid colouring is here obscured by the extension of the coloration to neighbouring structures which are flooded with anthocyanin.

**Petiveria alliacea** (14, pp. 91, 92, with Figs. 16-19; 18, p. 182, and 19b, pp. 208-212, with Fig. 11). T 4, diagonal, green A 4, orthogonal + 4 or fewer, diagonal G 2 median as in *Rivina humilis* (see above). Stigma brush-like, lateral, sessile. Fruit dry, indehiscent.

The subtending bract and pair of bracteoles are exerted immediately beneath the flower. Unlike those of *Rivina* and *Ledenbergia* (see above) they possess a midrib bundle. The formation of these three bundles in the anterior and lateral planes immediately before those for the perianth accounts for the very exceptional position of the tepals which, with their midrib bundles, lie on the alternate set of radii, i.e. in

the diagonal planes. The marginal veins of each tepal originate from the same sector of the central vascular cylinder as the corresponding midrib bundle. The tepals thus receiving their whole vascular system from the one set of sectors only are green. [The later paling of the green colour almost to white does not constitute an exception to the above interrelation, for the paling extends to the neighbouring structures and, like the opposite condition of 'flooding' with anthocyanin, as in *Ledenbergia*, is not, therefore, strictly a tepal characteristic.]

The lateral position of the stigma is due to the curvature of the sterile carpel through the upward development of the large ovule, which causes the apex of the carpel to be pushed over to one side. Since the sterile carpel midrib extends as far as the stigma, it also becomes curved. Hence in transverse sections of the upper region of the ovary this bundle is cut through twice.

#### PHYTOLACCEÆ

Flower ♀ or if unisexual with rudiments of the non-functional sex. Ovary of  $> 2$  carpels.

**Phytolacca** (14, pp. 82–84, with Figs. 1–5, and p. 94, Diagram A). Flower ♀. Tepals 5 with true lateral veins. [N.B.—The anthocyanin colouring sometimes present in the tepals is not limited to these members but extends to adjacent structures, hence it is not indicative of the vascular anatomy.] Stamens generally 10–20, rarely fewer or more numerous. Gynæceum syncarpous, becoming pseudo-apocarpous above, or, through suppression, apocarpous throughout.

**P. clavigera**, **P. decandra**. Gynæceum syncarpous becoming pseudo-apocarpous above.  $Gn + n$ , see p. 369.

**P. acinosa**, **P. dioica**. ♀ Gynæceum apocarpous through suppression.

#### GYROSTEMONEÆ

Flowers unisexual without rudiments of the non-functional sex. Ovary of  $> 2$  carpels.

**Gyrostemon australasicus** (14, pp. 85–89 with Figs. 10–12, and p. 94, Diagram C). ♂ Flower. T 5–8 with true lateral veins and hence not petaloid A 8–∞. ♀ Flower. T 5–8 as

in the ♂, G generally 5-8, solid, fertile + 5-8, semi-solid, sterile. Ovary multilocular becoming pseudo-apocarpous through very early splitting of the sterile carpels from without inwards, thus giving rise to segments of  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels, the segments being retained in position through fusion of the inner portion of the carpels with the central parenchyma of the axis which is prolonged to the level of the styles. Fruit dehiscent in the mid-line of the sterile carpels.

The outer carpel midribs turn inwards as the loculi close above, and gather up in their course half the vascular system of the inner sterile carpel on each side. Hence each style receives a single vascular cord corresponding with the fused systems of  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels.

**Codonocarpus cotinifolius** (14, pp. 85-88 with Figs. 6-9). Perianth as in *Gyrostemon* (see above), G generally  $\infty$ , of valve form and fertile + as many solid and sterile, otherwise as in *Gyrostemon*.

## 119. AIZOACEÆ

Flower ♂, actinomorphic, hypogynous (*e.g.* *Mollugo*, *Glinus*, *Aizoon*) or more or less syngonous (*e.g.* *Tetragonia*, *Mesembryanthemum*). Perianth generally single, rarely differentiated into calyx and corolla (*e.g.* *Macarthuria australis* with entire petals, *Mesembryanthemum* with  $\infty$  petaloid structures through multiplication), pentamerous or tetramerous. Stamens equal in number with the tepals and alternating with them, or fewer by suppression, or more numerous through multiplication and then sometimes united in bundles. Carpels in two whorls, 3-5-6-(-8-20) + 3-5-6-(-8-20), the one whorl sterile, the other fertile. Outer carpels when equal in number to the tepals or sepals superposed upon them. Ovary with as many loculi as outer carpels (or fewer by confluence). Styles (when distinct) and stigmas as many as the outer carpels and standing over these carpels. Ovules solitary- $\infty$  and multiseriate in each loculus. Fruit a capsule dehiscing loculicidally or septicidally or by a lid, or nut-like, or drupaceous.

Tepals with commissural marginal veins and hence coloured throughout or with non-green margins (see Vol. I, Introduction, p. 10; also 19*a* and 19*b*, pp. 208 and 213. For references to other examples see in the present Volume under *Phytolaccaceæ*, Part 10, p. 371.).

## ILLUSTRATIVE TYPES

***Tetragonia*** (*e.g.* *T. expansa*). Flower syngonous. Generally T 4, coloured A 4<sub>3</sub> G 6-8, sterile + 6-8, fertile. Ovules solitary in each loculus. Fruit nut-like or drupaceous.

***Mesembryanthemum*** (*e.g.* *M. edule*, *M. serratum*, *M. violaceum*). Flower syngonous. K 5, green C 5 $\infty$  A 5 $\infty$  G 5, fertile + 5, sterile. Ovary 10-locular below,

shortly becoming 5-locular. Ovules multiseriate in each loculus. Fruit capsule-like.

The ovary is exceptional in that it is the whorl of carpels in line with the loculi which is fertile and the alternate one which is sterile. In this respect it resembles Geraniaceæ (see under this Family in Vol. I, Part 3, p. 70 and in this Volume, p. 580†) and *Phytolacca* (see under Phytolaccaceæ earlier in the present Volume, Part 10, p. 368). Furthermore, each placenta, which at first forms a complete septum, is immediately withdrawn from the centre towards the outer wall of the loculus so that except at the extreme base the ovules appear to be borne on the midribs of the fertile carpels. In this feature it finds probably its only parallel in *Punica* (see under Punicaceæ earlier in the present Volume, Part 8, p. 277). [The withdrawal from the centre of carpels which at first form complete septa is not uncommon, but elsewhere, when both sterile and fertile carpels constitute complete partitions, it is the sterile carpels which become withdrawn and the fertile carpels which continue to divide up the cavity of the ovary as, *e.g.* in Linaceæ (see under that Family in Vol. I, Part 3, p. 77 and in this Volume, p. 580†).]

**Aizoon spp.** Flower hypogynous. T 5, coloured A 5<sub>∞</sub> in bundles G 5, sterile + 5, fertile. Fruit a capsule, dehiscing loculicidally.

Tepals with commissural marginal veins.

## 120. BASELLACEÆ

Flower ♀, actinomorphic, hypogynous. K segments 2 C 5, quincuncially arranged. A 5, antepetalous G (in its fullest development) 6 (3 + 3) standing in one ring, sterile + 1 or ? more, potentially, but only 1 actually fertile. Ovary unilocular. Ovule solitary, basal. Style single. Stigmas distinct and filamentous or united and capitate. Fruit enclosed in the perianth, one-seeded, dry or succulent, indehiscent.

## ILLUSTRATIVE TYPES

**Basella.** K segments 2 C 5 A 5, antepetalous G 6, sterile + 1, fertile (see below) Style short. Stigmas 3, filamentous, papillose on their inner face, standing over three alternate carpels of the sterile whorl. Fruit succulent.

Six main vascular cords turn outwards from the enlarged central cylinder at the flower base leaving residual elements behind in the centre. These residual groups of elements are organised into a corresponding number of sterile carpel midribs. Three of these bundles are continued into the style and stigmas, those of the three alternate carpels come to an end as the loculus closes. The six primary out-turning bundles at the base break up variously according to their radial position, giving rise by lateral branching to the midribs and secondary veins of the two calyx segments and by centripetal sub-division to the midribs and pair of primary laterals of each petal and to the five stamen bundles, hence the superposition of the stamens upon the petals. The undifferentiated vascular strand which serves the ovule is single in origin and unconnected before fertilisation with the vascular system of the ovary wall. It is therefore uncertain whether it should be regarded as representing a single carpel or as being derived from the 'condensed' systems of three carpels. The whole vascular system of the gynæceum thus shows a further stage in reduction than that of trimerous cyclic types in Polygonaceæ, such as *Rheum*, since in this latter genus there is evidence that the single central fertile vascular column results from the 'condensation' of the vascular units proper to three potentially fertile carpels (see under Polygonaceæ earlier in the present Volume, Part 10, p. 354).

## 121. CERATOPHYLLACEÆ

Flowers unisexual, monœcious. Perianth segments united at the base. ♂ Flower. Perianth segments generally about 12. A 10-20. ♀ Flower hypogynous. Perianth segments generally 8-10. Ovary unilocular. Ovule solitary, pendulous from the top of the loculus. Style single, terminal, slightly kinked at the level at which the fertile carpel ends in a small lip or blunt process while the receptive sterile carpel continues upwards. Fruit one-seeded, indehiscent, sometimes with a pair of opposite spines at the base, sometimes with a flange or wing extending vertically in line with each spine above and below.

The flowers are without differentiated vascular elements. In the ♀ the gynœceum is strictly terminal. As the laterally compressed ovary becomes disjoined from the base of the perianth cup, undifferentiated vascular elements turn out from the centre, forming a dorsal and a ventral strand. The loculus then makes its appearance in the central area of parenchyma. At the top of the ovary the short funicle takes its rise from the ventral mid-line, the loculus closes and the ovary passes without a definite boundary directly into the style. The strictly terminal position of the ovary, the form of the style, the symmetrical mode of origin and disposition of the two undifferentiated vascular strands, and the symmetrical arrangement of the spines and wings on the fruit in some species all point to a construction from two carpels, one dorsal, sterile, one ventral, fertile.

## ILLUSTRATIVE TYPES

\**Ceratophyllum* (Hornwort). See the characters of the Family.

\**C. submersum*. Fruit without spines or wings.

\**C. demersum*. Fruit with two median spines (one dorsal, one ventral).

## 122. TROCHODENDRACEÆ

Flowers ♂, polygamous or diœcious, hemicyclic, hypogynous or perigynous, without perianth. A spiral,  $\infty$ . G cyclic, 2-numerous, sterile + 2-numerous, fertile. Ovary syncarpous and multilocular below where the fertile carpels extend to the central parenchyma of the axis, becoming pseudo-apocarpous above after the central parenchyma has come to an end and as the fertile carpels, after having become free on their inner face, undergo median radial splitting from without inwards. Ovules numerous in each loculus in two or in several rows, or solitary. Styles and stigmas as many as the sterile carpels and centred over these carpels. Partial fruits several-seeded and dehiscent or one-seeded and indehiscent.

## ILLUSTRATIVE TYPES

**Trochodendron aralioides.** Flower ♂, perigynous. K o C o A spiral,  $\infty$  G cyclic, 5-8 or more, sterile + 5-8 or more, fertile. Styles and stigmas of  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels. Stigmas zygomorphic, grooved, as frequently when thus constituted. Ovules numerous, in several rows in each loculus. Fruit partially sunk in the fleshy axis. Partial fruits dehiscent.

The vascular bundles for the  $\infty$  stamens are derived by branching from a smaller number of primary cords which turn out successively from the central cylinder. Sterile carpels with typical valve carpel venation (a midrib and pair of primary laterals). Fertile carpels without separate midrib bundles. Sterile carpel midribs and fertile carpel placental bundles prolonged to the stigma level.



## 123. ANONACEÆ

Flowers ♂ or less often unisexual, hemicyclic, actinomorphic, hypogynous or vary rarely perigynous. Perianth generally of three trimerous whorls. Stamens generally  $\infty$  and spiral, seldom few. Gynæceum with one exception (*Monodora*) apocarpous. Ovaries monocarpellary, generally  $\infty$  and spiral, seldom only 5 or 3. Ovules springing from the ventral suture and then generally numerous, seldom solitary; or 1 or 2 basal. Individual fruits generally separate berries; sometimes all the ovaries together with the axis form a single fleshy compound fruit (pseudocarp).

## ILLUSTRATIVE TYPES

**Asimina triloba.** Flower ♂. K 3 C 3 + 3 A  $\infty$ , spiral G apocarpous 3-15, spiral. Ovaries monocarpellary. Ovules numerous.

As in other monocarpellary types the ovary wall becomes cleft at the level of appearance of the loculus which thus communicates with the exterior at this level.

**Monodora grandiflora.** Flower ♂. K 3 C 3 + 3 A  $\infty$  G 2, syncarpous, 1 solid and sterile, 1 semi-solid and fertile. Ovary unilocular. Ovules scattered over almost the whole inner surface of the ovary wall, being supplied by the copiously branched system of the fertile carpel. Stigmas sessile, confluent, crowning both carpels, forming a zygomorphic, convoluted crest. Fruit a berry.

The ovary is furrowed or cleft at the summit in the mid-line of the fertile carpel. The extension of this cleavage causes the stigmatic crest to be crescent-shaped, the crescent being centred over the sterile carpel and constructed of  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels.

In the exceptional syncarpous form of the gynæceum *Monodora* stands in the same relation to other genera in the Family as *Actæa* to other genera in Ranunculaceæ (see under that Family in Vol. I, Part 2, p. 35).

## 124. CALYCANTHACEÆ

Flowers ♂, perigynous, borne singly on the end of the cup-shaped floral axes, actinomorphic, acyclic.  $T\infty$  A 10–30, the inner ones staminodal G (about) 20 lining the lower portion of the 'cup,' apocarpous. Ovaries monocarpellary, containing two ovules. Styles and stigmas furrowed along the ventral face. Whole fruit, a collection of achenes.

## ILLUSTRATIVE TYPES

**Calycanthus spp.** See the characters of the Family. About thirteen stamens fertile.

Each tepal receives in addition to the midrib bundle a pair of primary laterals which, although the perianth is acyclic, can properly be regarded as commissural in origin, since they do not arise from the midribs of the tepals which they enter, but are detached just below the exertion level from the neighbouring cord on either side, which furnishes the midrib bundle of another tepal exerted at a different level.

Each ovary (carpel) receives a single bundle which becomes the midrib from which the single placental strand is detached. This is most readily established for the central ovaries, for as these ovaries stand upright transverse sections taken through the floor of the axial 'cup' also cut the vascular supply to these ovaries transversely. Shortly after the division of the placental strand into twin bundles the loculus makes its appearance and at once becomes continuous with the exterior through a channel passing between the two placental bundles, as commonly in monocarpellary ovaries and in bicarpellary ovaries in which the fertile carpel lacks a separate median bundle (see the several Families cited earlier in the present Volume under Phytolaccaceæ, Part 10, p. 370). The ovary wall immediately becomes resealed above this level as the carpel edges become reunited.

**Chimonanthus fragrans.** See the characters of the Family. Only five stamens fertile.

## 125. MONIMIACEÆ

Flowers ♂ or more often through abortion unisexual, monœcious or diœcious, perigynous, almost always actinomorphic, generally hemicyclic or acyclic. Tepals few or numerous, less often wanting, the outer sometimes sepaloid the inner petaloid. Stamens generally  $\infty$ , without definite arrangement, or less numerous and in one or two series. Gynæceum apocarpous. Ovaries generally numerous, monocarpellary. Ovules solitary, basal. Fruit often spurious through the envelopment of the whole group of separate ovaries by the axis which undergoes further growth after fertilisation (pseudocarp). Individual fruits drupaceous or nut-like.

## ILLUSTRATIVE TYPES

**Laurella novæ-zelandiæ.** Flowers diœcious or polygamous. ♂ Flower. Perianth members 5 or 6, stamens about 12. ♀ and ♂ Flowers. Staminial members (all staminodal or staminodes together with some stamens) and carpels (ovaries) 6–12, in two or three rows. Individual fruits achenes enclosed in a cupule formed of axis tissue which splits into two or three valves.

The stamens and carpels are borne on the sides and base of the concave receptacle, respectively.

The central vascular cylinder of the axis enlarges below the flower, breaking up into a ring of numerous bundles. Branches detached successively from these primary bundles turn inwards and become the midrib bundles of a corresponding number of carpels, each of these detached bundles giving rise at once and below the locus to a placental strand. At a higher level more branches given off irregularly from the same primary bundles serve the stamens which spring from the sides of the concave receptacle. The residual bundles are used up in furnishing the bundles for the perianth members which spring from the rim of the receptacle.

The ovary wall, as commonly in ovaries of one carpel (sometimes also in those of two carpels) becomes cleft in the ventral mid-line so that the loculus communicates with the exterior. (For a more detailed statement see earlier in the present Volume under Phytolaccaceæ, Part 10, p. 370.) In *Laurelia* this opening is not closed but continues as a furrow up to the base of the plumose style.

## 126. LAURACEÆ

Flowers ♂ or unisexual by abortion but usually with rudiments of the non-functional sex, actinomorphic, hypogynous or slightly perigynous. Perianth of 2 whorls (see below), andrœcium of 3 or 4 (very rarely of 5), generally trimerous, sometimes dimerous, rarely tetramerous whorls. One or more of the stamen whorls, generally the innermost, rarely the outermost, staminodal. Filaments united at the base with the perianth; those of one or more inner whorls often with paired vascular glandular structures (see below). Gynœceum syncarpous. Carpels varying in number from (probably) 3-1 sterile + 3-1 fertile. When reduced to 2 (1 + 1) the sterile member posterior, the fertile member anterior (see below). Ovary unilocular. Ovule solitary, pendulous from the front wall of the loculus (see below). Style single. Stigma distinctly or obscurely lobed, lobes equal in number to the sterile carpels, and standing over these carpels. When only one sterile carpel is present the single stigma has the grooved zygomorphic form often characterising the single valve carpel, for in this Family the fertile carpel comes to an end at the level of origin of the ovule. Fruit a berry or drupaceous.

The perianth of four members and also that of six members arises in two whorls. When four, the members lie in the orthogonal planes. Development of the sepals or tepals of a tetramerous perianth in two successive pairs is usual (see under Cruciferae and Nepenthaceae in Vol. I, Part 2, p. 41, and Part 4, p. 128, respectively; and earlier in the present Volume under *Hydrangea* (Saxifragaceae), Part 5, p. 149; Tamaricaceae, Part 7, p. 247; Urticaceae, Part 9, p. 338, and *Rivina* (Phytolaccaceae), Part 10, p. 370; and later in the present Volume under Ericaceae and Sapotaceae, Part 11, pp. 394 and 415, respectively). As a rule, the median is the outer pair, but in Lauraceae the lateral pair is the outer as it also is in *Ascyrum* (see under Guttiferæ, Part 7, p. 242).

The alternation of successive dimerous whorls in the orthogonal planes is generally continued in the andrœcium, the outermost being lateral, the next median and so on alternately. Exceptionally, the two dimerous perianth whorls are treated as a single tetramerous whorl by the outermost staminal whorl, the four members of which lie in the diagonal planes. But this tetramerous scheme is not as a rule maintained. The later whorls return to the dimerous ground-plan, standing alternately in the lateral and the median planes.

The central vascular cylinder becomes enlarged at the flower base and usually consists of a large number of very small strands. From this cylinder the bundles for the tepals and stamens turn outwards. In the ♀ and ♂ flowers residual elements left behind on all the radii turn inwards to become organised later into the carpel bundles. This break-up of the cylinder has the result that the tepals generally receive, in addition to the midrib bundle, one or two pairs of separate lateral veins which (possibly) represent laterals of commissural origin, being derived from a vascular unit which also furnishes a stamen bundle.

The vascular system of the andrœcium is remarkable in that whereas the staminodes in the ♀ flower, even when as large as a functional stamen, receive only a single bundle, the filaments of the 'gland-bearing' stamens in the ♂ flower receive a triplet of strands if a 'gland' is developed on each side, two strands if only one lateral 'gland' is formed. One strand in both cases serves the functional anther, the additional strand(s) the so-called 'gland(s)'. If additional strands enter a 'glandless' stamen of a male flower they either remain undifferentiated or cease below the 'gland' level. These glandular structures vary in form in different genera; in some they take the form of a filament ending in an anther-shaped but pollenless enlargement. The above facts indicate that in ♂ flowers the staminal members of some, or sometimes of all the whorls undergo multiplication and that the so-called 'glands' represent aborted stamens produced in this way (unpublished). The vascular development within the 'gland' also accords with this interpretation.

For the single vascular bundle of the 'stalk' on entering the 'gland' divides in two, the two branches diverging into the two halves corresponding with the two modified thecæ, each branch ending in an enlarged brush-like complex comparable with that formed in the cushion-like staminodes of *Clavija* (Theophrastaceæ) (see 22, p. 133, Fig. 4).

The residual vascular elements for the gynæceum form a complete cylinder. It may therefore be inferred that the two carpels of the dimerous gynæcea result from reduction from a larger number. In these gynæcea the posterior sterile carpel is of the valve type with a midrib bundle and a pair of true lateral veins; the anterior carpel is of the solid type with an unbranched bundle. As generally in this type of ovary when the fertile carpel comes to an end at the level of origin of the ovule the loculus communicates at this level with the exterior, until the edges of the sterile carpels come together and unite above the opening (for other instances see those cited earlier in the present Volume under the section Riviniæ of the Phytolaccaceæ, Part 10, p. 370).

The anterior position of the ovule leaves no doubt that the gynæceum is composed of more than one carpel, for in the monocarpellary ovary the carpel is always turned with its edges towards the back.

### ILLUSTRATIVE TYPES

**Laurus nobilis** (Bay-tree). Flowers unisexual or polygamous, dioecious. ♀ Flower. Androecium staminodal.

♂ Flower. T (generally) 2 + 2, orthogonal A 4, diagonal + (generally) 2 triplets + 2 triplets + 2 triplets, all orthogonal, alternately median and lateral, each consisting of one fertile stamen flanked on each side by an

aborted modified stamen (so-called gland) and furnished with three vascular strands, G rudimentary.

♀ Flower. T (generally)  $2 + 2$ , orthogonal A 4, diagonal, each with a single vascular bundle G 2, one posterior, sterile, of valve form with midrib and a pair of lateral veins, one anterior, fertile, solid with midrib only. Style with one vascular bundle (midrib of the sterile carpel). Stigma grooved, zygomorphic. Fruit a berry.

**Cassytha.** Flower ♂. K 3 C 3 A 3, each with a single vascular bundle + 3, each with a single vascular bundle + 3 triplets, each with three vascular bundles + 3, each with a single vascular bundle G 2, one sterile, one fertile. Fruit enclosed in the perianth tube, which becomes fleshy.



## Part II

### Dicotyledons

Family	127.	Clethraceæ
„	128.	Pirolaceæ
„	129.	Ericaceæ
„	130.	Epacridaceæ
„	131.	Theophrastaceæ
„	132.	Myrsinaceæ
„	133.	Primulaceæ
„	134.	Plumbaginaceæ
„	135.	Sapotaceæ
„	136.	Ebenaceæ
„	137.	Styracaceæ



## 127. CLETHRACEÆ

Flower ♂, actinomorphic, hypogynous, pentamerous in the outer whorls but with a trimerous gynæceum. (K 5 C 5 A 5 + 5 G 3, sterile + 3, fertile.) No disc present. Gynæceum syncarpous, ovary trilocular, the fertile carpels reaching to the centre. Style single, sunk in the concave top of the ovary, dividing above into three stigmatic arms through radial splitting of the fertile carpels. The arms, each of  $\frac{1}{2}$  +  $\frac{1}{2}$  carpels, stand over the sterile carpels. In this position of the stigmas *Clethra*, the only genus, differs from all genera in the related Families Pirolaceæ and Ericaceæ which have 'commissural' stigma lobes (see later in the present Volume, Part II, p. 390 and p. 393, respectively). Ovules  $\infty$ , in numerous rows on each placenta. Fruit a 3-valved capsule, dehiscing loculicidally through median radial splitting of the sterile carpels and septifragally by the tearing of the tissue of the fertile carpels (septa) so as to leave a central column of the conjoined placentæ bearing the seeds.

Sepals with true lateral veins.

### ILLUSTRATIVE TYPES

**Clethra.** See the characters of the Family.

## 128. PIROLACEÆ

Flower ♂, actinomorphic, hypogynous, isomerous throughout, generally pentamerous or tetramerous, six-whorled, obdiplostemonous, with antepetalous loculi. (K 4 or 5 C 4 or 5 A 4 or 5 + 4 or 5 G 4 or 5, sterile, antepetalous + 4 or 5, fertile, antesepalous.) Disc in the form of a 10-toothed ring, or of ten distinct glands, or absent. Stamens free from the corolla. Gynæceum syncarpous. Ovary multilocular below where the fertile carpels extend to the centre, becoming unilocular above as these carpels separate from one another along their inner face (16†), or exceptionally, unilocular throughout. Placentæ sometimes so large that the adjacent placentæ of two neighbouring fertile carpels come to occupy the greater part of the area of each loculus in the ovule-bearing region of the ovary and form a continuous mass of tissue, the two component placentæ only becoming defined towards the summit of the ovary (as in *Monotropa* and to a less extent in *Pirola*). A similar lack of demarcation in somewhat comparable circumstances is characteristic of many Caryophyllaceæ (see under *Cucubalus baccifer* in that Family, Vol. I, Part 4, p. 103). Style single, sunk in a depression at the summit of the ovary. Stigma terminal, entire or with lobes as many as the fertile carpels and standing over these carpels ('commissural'). Ovules ∞, in numerous rows on each placenta. Fruit a capsule, dehiscing loculicidally through median radial splitting of the sterile carpels.

## ILLUSTRATIVE TYPES

\**Monotropa* (16, pp. 114, 115, and p. 98, Figs. 72-82). Saprophyte. Flower generally 5-, sometimes 4- or less often 6-merous. Disc in the form of non-vascular glands

alternating with the stamens. Ovary multilocular below, becoming unilocular above. Styler canal, 5-rayed at the base, the rays standing over the loculi; becoming 10-rayed above as the intervening placental cushion of each fertile carpel begins to split radially from within outwards; enlarging and opening upwards as the style passes into the 5-angled, funnel-shaped stigma with its entire, papillose rim.

**\*M. Hypopitys.** (Yellow Bird's nest.) Flowers 5- or 4-merous.

**M. uniflora.** Flowers 5- or 6-merous.

The vascular scheme is diagrammatic in its regularity and simplicity. After the sepal midrib bundles have turned outwards from the centre the residual system consists of a ring of ten trunk cords. Each cord on a petal radius breaks up at once into a petal midrib, an antepetalous stamen bundle and a sterile carpel bundle, each of those on a sepal radius similarly into an antesepalous stamen bundle and a placental bundle, the fertile carpels having no separate midrib bundle. Thus, in a single transverse section, at the appropriate level, these twenty-five bundles appear disposed, as it might be, on a ten-spoked wheel, three bundles and two bundles occurring on the alternate spokes. Only the sterile carpel midribs are prolonged into the style, one midrib bundle running upwards in line with each of the five canal rays.

**\*Pirola** (Wintergreen). Flowers 5-merous. Disc present or absent. Ovary multilocular. Style long, enlarging at the top where it forms a slightly revolute rim or collar derived from both sterile and fertile carpels. Above this rim project five erect teeth or lobes representing prolongations of the placental cushions of the fertile carpels, between which the styler canal opens to the surface. The collar as well as the lobes usually become covered with a sticky secretion, so that doubtless, ordinarily, the whole surface may be receptive.

**\*P. minor, \*P. media, \*P. rotundifolia.** Disc wanting.

**\*P. secunda.** Disc in the form of ten glands alternating with the stamens.

**\*P. (Moneses) uniflora.** Disc in the form of a 10-toothed ring.

The vascular system differs from that of *Monotropa* (see above) in that the midrib bundles for the several whorls turn outwards from a central cylinder separately and successively. Midrib bundles are present in the fertile as well as in the sterile carpels. Both sets of bundles are continued up into the style, as also are the five placental bundles—an unusual feature, fertile carpel midrib and placental bundles rarely remaining separate above the top of the ovary. As the stigma level is approached the ten midrib bundles turn out horizontally, coming to an end in the slightly revolute rim, while the placental bundles continue upwards into the corresponding teeth or lobes.

**Chimaphila.** Flower 5-merous. Ovary multilocular below, becoming unilocular above as the fertile carpels fail to reach the centre. Style short, thick, ending in a flat, five-angled plate on which the stylar canal opens to the surface in five rays in line with the sterile carpels and loculi, the stigmatic lobes lying over the fertile carpels on the alternate radii. As the sterile and fertile carpels terminate at the same level the 'commissural' stigmatic lobes project horizontally from the rim of the terminal plate inwards instead of standing vertically upwards through extension of the fertile carpels above the rim as in *Pirola* (see above).

Sterile and fertile carpel vascular bundles extend to the stigma level, but as the placental bundles do not remain distinct from the midrib bundles of the fertile carpels, only ten bundles traverse the style in place of the fifteen bundles present in *Pirola* (see above).

## 129. ERICACEÆ

Flower ♂, actinomorphic or rarely slightly zygomorphic, hypogynous or syngonous, almost always isomeric throughout and either pentamerous or tetramerous, very rarely trimerous, six-whorled (K 4 or 5 C 4 or 5 A 4 or 5 + 4 or 5 G 4 or 5, sterile + 4 or 5, fertile) (I, p. 475) or exceptionally five-whorled through suppression of the antepetalous stamen whorl, very rarely with a complete antepetalous whorl combined with reduction in the antesealous whorl. When isomeric and six-whorled obdiplostemonous (28, p. 308). Filaments free or epipetalous. Beneath and between the filaments and surrounding the ovary a ring-shaped disc. Gynæceum syncarpous. Ovary multilocular through fusion of the fertile carpels on their inner face with the prolonged central parenchyma of the axis, sometimes becoming unilocular above as this parenchyma comes to an end and the fertile carpels become free on their inner face. Loculi antepetalous with rarely one, generally numerous, ovules in each loculus. Placentæ sometimes so large as to be confluent, only becoming distinct towards the top of the ovary (*Erica* spp., *Tripetaleia*, *Vaccinium*, *Rhododendron*) as in Pirolaceæ (see under that Family earlier in the present Volume, Part II, p. 390). Style single, sunk in a depression at the top of the ovary. Stigma terminal with lobes or sectors as many as the fertile carpels and standing in line with these carpels ('commissural'); sometimes surrounded by a distinct rim as in Pirolaceæ (see under that Family, *loc. cit.*). Very rarely with twice the above number of lobes, half the number standing over the sterile and half over the fertile carpels, as in *Leucothoë* in which the style of the pentamerous gynæceum ends in a ring of ten stigmatic lobes, all alike and all arising at the same level; and as in the more striking example of

*Tripetaleia* in which the stigma lobes of sterile and fertile carpels are of different form (see below under Illustrative Types). In this exceptional development these two genera thus bear the same relation to the rest of Ericaceæ, as *Aphyllanthes* and *Aspidistra* among Liliaceæ to the rest of that Family (see Vol. I, Part 2, p. 65; also 8, pp. 58–60 and p. 56, Figs. 49–54); and among types where styles as well as stigmas are distinct as the Ureneæ to the rest of Malvaceæ (see under that Family, Vol. I, Part 4, pp. 107–110, also 27 with numerous Figs.); and as the ♀ flowers of Pæpalanthoideæ among Eriocaulaceæ to those of *Eriocaulon* (see under this Family later in the present Volume, Part 16, p. 558). Fruit in hypogynous types almost always a capsule with loculicidal or septicidal combined with septifragal dehiscence so that the valves fall away from the seed-bearing central column.

Sepals in tetramerous forms, as in most other types with K 4, in two pairs (for other instances see those cited earlier in the present Volume, Part 10, p. 383). In some forms in which the symmetry of the floral vascular ground-plan is disturbed by the near neighbourhood of the vascular bundles for the subtending bract and pair of bracteoles, the four sepal midrib bundles may turn outwards at three different levels (see 18, pp. 179–182†). In the pentamerous types the calyx is generally valvate, but some in which it is quincuncial, e.g. *Rhododendron racemosum*, afford examples in which the spiral sequence is particularly clear owing to the marked difference in level at which the midrib bundles turn out from the central vascular cylinder (see below under Illustrative Types, p. 396, Fig. 18 A, B, and later in the present Volume under Epacridaceæ, Part 11, Fig. 20 A, B).

Marginal veins of the sepals, when present, not commissural, but derived by branching from the midrib (see 19b, p. 202, Fig. 2). The vascular bundles for the antesepalous stamens usually turn out independently, those for the antepetalous stamens sometimes also independently (e.g. *Erica*), sometimes conjoined with the petal midribs into one set of trunk cords (e.g. *Rhododendron* spp.). The midrib bundles of the sterile carpels well-developed, those of the fertile carpels generally soon coming to an end or wanting. Only the sterile carpel bundles, as a rule, are prolonged up the style.



## ILLUSTRATIVE TYPES

**\*Erica spp.** (Heath). Flower hypogynous, actinomorphic, six-whorled generally tetramerous, obdiplostemonous. Loculi antepetalous. Style slightly enlarged at the top as in Pirolaceæ (see under that Family earlier in the present Volume, Part II, p. 391), but the precise form varying with the relative prominence of the annular rim and of the apical lobes, both structures being generally less developed than in the above-mentioned Family. Fruit a capsule, dehiscing loculicidally and septifragally.

The vascular bundles for both stamen whorls originate independently from the central cylinder. The antepetalous position of the loculi is attributed to a state of 'congestion' envisaged as being set up under these conditions (see Vol. I, Introduction, pp. 8, 9).

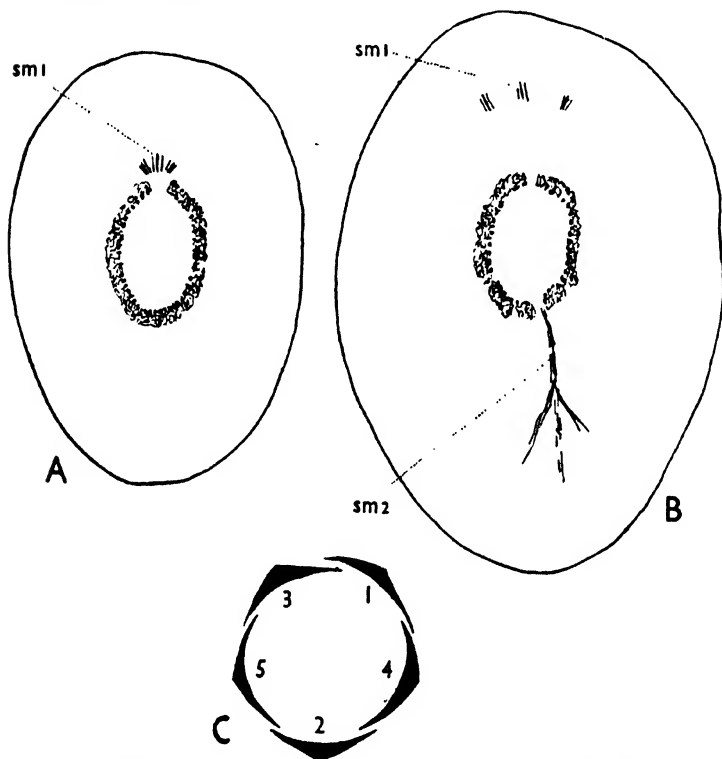
**\*Calluna vulgaris** (Heather, Ling). Flower as in *Erica* (see above). Fruit a capsule dehiscing septicidally and septifragally.

**Rhododendron spp.** (e.g. *R. racemosum*) (see Fig. 18; also 28, p. 308). Flower hypogynous, slightly zygomorphic, six-whorled, pentamerous, obdiplostemonous. Ovary multilocular below, becoming unilocular above as the fertile carpels become free on their inner face. Loculi antepetalous. Fruit a capsule, dehiscing septicidally and septifragally.

Calyx quincuncial with sepal 2 to the front (see Fig. 18 C), thus differing from most other pentamerous genera in the present and in other Families in which sepal 2 is posterior (see earlier in the present Volume, Part 5, p. 149, Fig. 7).

The vascular bundles for the antesealous stamens originate independently, but those for the antepetalous stamens are carried out conjoined with the petal midrib bundles. In these circumstances the antepetalous position of the loculi is not due to the state of 'congestion' envisaged as the cause in other six-whorled types, in which the vascular bundles for all the whorls arise independently (see Vol. I, Introduction, pp. 8, 9), but results from a ground-plan in which the antepetalous stamen bundles are not detached from the petal-stamen trunk

ords until these cords have reached points further from the centre than those reached at the same level by the antesealous stamen bundles.

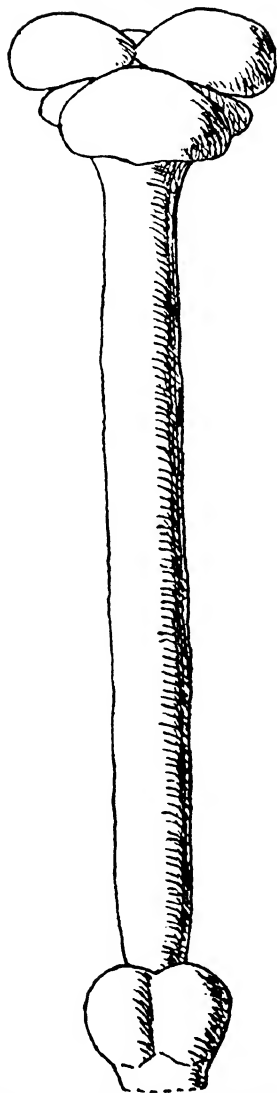


*Rhododendron racemosum*. Transverse sections through the flower base. A, at the level of origin of the midrib bundle for sepal 1. B, at the level of origin of the midrib bundle for sepal 2; midrib bundles with true lateral veins. C, diagram of the quincuncial arrangement, in the unusual case in which sepal 2 is anterior. The direction of the spiral is shown as clockwise.

FIGURE 18.

**R. indicum.** Flower five-whorled through suppression of the antepetalous stamen whorl, otherwise as *R. racemosum* (see above).

Since the vascular bundles of the antepetalous staminal whorl, when present, do not arise independently, the suppression of this whorl does not affect the radial position of the



*Tripetaleia paniculata*. The ovary, style and stigma (greatly enlarged).

FIGURE 19.

carpels and loculi which, as in the preceding species, are antepetalous.

**\*Vaccinium spp.** (*e.g.* \**V. Myrtillus*, Bilberry; \**V. Vitis-idaea*, Red Whortleberry; \**V. Oxycoccus*, Cranberry). Flower syngonous. Fruit a berry.

***Tripetaleia paniculata*** (Fig. 19). A 'key' genus (see above under the characters of the Family). Flower hypogynous, trimerous. Ovary becoming unilocular above as the central parenchyma of the axis comes to an end and the fertile carpels become free on their inner face. Stigma 6-lobed, three lobes standing over the sterile, and three over the fertile carpels. Fruit a capsule, splitting septicidally and septifragally.

***Leucothoë Catesbæi***. Flower in the main as in *Erica* (see above), but stigma lobes 10.

Style with five vascular bundles representing the sterile carpel midribs as in *Erica*. But at the level of the stigmas the five fertile carpel bundles reappear, hence the formation of a ring of ten stigma lobes in correspondence with the ring of ten vascular bundles.

## 130. EPACRIDACEÆ

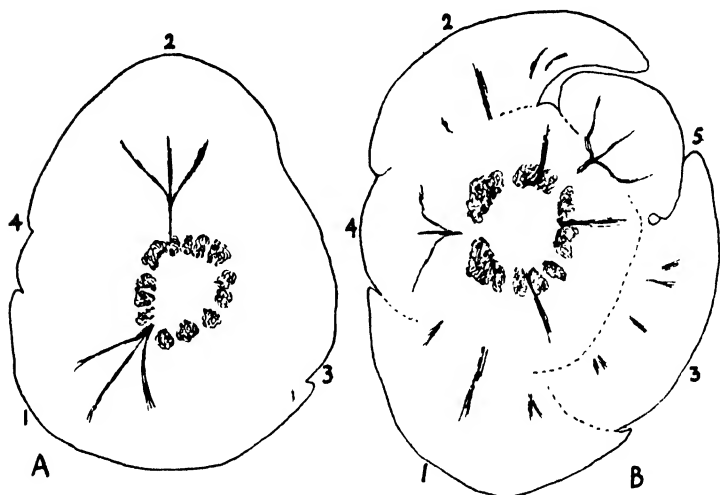
Flower ♂, actinomorphic, hypogynous, almost always isomerous and pentamerous, five-whorled through absence of an antepetalous stamen whorl (K 5 C 5 A 5 G 5, sterile, antepetalous + 5, fertile, antesepalous). A disc usually present in the form of an entire or five-lappeted cup- or ring-shaped structure, or as five separate glands. Gynæceum syncarpous. Ovary multilocular through fusion of the fertile carpels, or rarely of both sterile and fertile carpels on their inner face with the prolonged central parenchyma of the axis, sometimes becoming unilocular above, as in Ericaceæ (see under that Family earlier in the present Volume, Part II, p. 393), as the parenchyma comes to an end and the carpels become free on their inner face (*e.g.* *Dracophyllum secundum*). Loculi, when isomerous with the perianth whorls, antepetalous. Ovules in several rows on each placenta or solitary in each loculus. Placentæ often continuous and undefined below, becoming distinct above (see similar feature in Ericaceæ, *loc. cit.*, p. 393). Style single, generally sunk in the concave summit of the ovary, less often terminal. Stigma terminal, when distinctly lobed with the lobes standing over the fertile carpels ('commissural'). Fruit generally a many-seeded capsule with loculicidal combined with septifragal dehiscence so that the five valves fall away from the seed-carrying central column; or drupaceous with one seed in each loculus and indehiscent.

Calyx quincuncial, with sepal 2 in the usual position at the back (Fig. 20; see also earlier in the present Volume, Part 5, p. 149, Fig. 7).

Sepals with lateral veins derived by branching from the midrib (Fig. 20 A, also 19b, p. 202, Fig. 2). Both sterile and fertile carpels generally with midrib bundles, but only those of the sterile members are prolonged up the style. The stigmatic lobes, when distinct, alternate with these bundles and hence stand over the fertile carpels ('commissural').

## ILLUSTRATIVE TYPES

**Epacris** (Fig. 20 A, B). Stamens epipetalous. Style sunk in the summit of the ovary. Ovules in several rows on each placenta. Fruit a capsule.



*Epacris longiflora*. Transverse sections through the flower base. A, at the level of origin of the midrib bundles for sepals 1 and 2. B, after the midrib bundles of all five sepals have turned out from the central vascular cylinder.

FIGURE 20.

**Dracophyllum spp.** Stamens free from the corolla. Styles, ovules and fruit as in *Epacris* (see above).

**Leucopogon spp.** Stamens epipetalous. Style terminal. Ovules solitary in each loculus. G 2-5, sterile + 2-5 fertile. Fruit drupaceous.

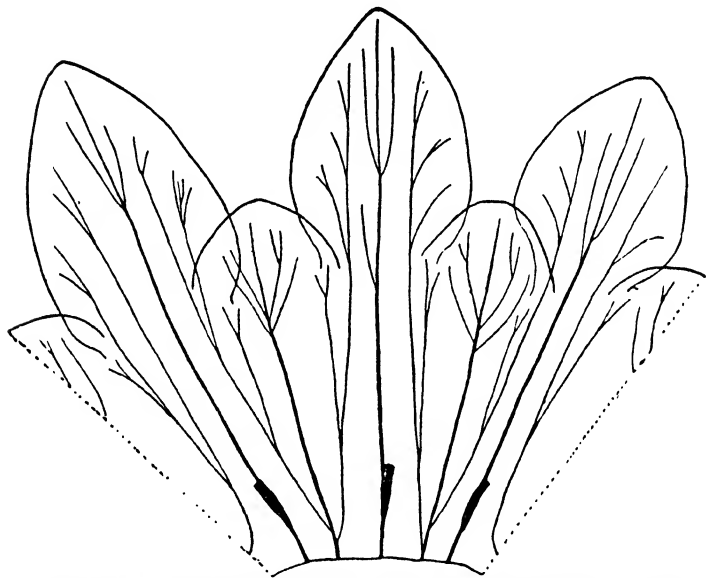
## 131. THEOPHRASTACEÆ

Flowers ♂ or, exceptionally, polygamous and dioecious (*Clavija*), actinomorphic, hypogynous, generally pentamerous, rarely tetramerous (*Clavija spp.*). Androecium in two whorls. Antesepalous members reduced to staminodes of various forms. Sometimes cushion-like. Sometimes incorporated into the corolla as petaloid sectors alternating with the true petal lobes as in *Jacquinia* (see Fig. 21); as also in *Soldanella* among Primulaceæ (see under that Family later in the present Volume, Part 11, p. 408, Fig. 24; also 22, p. 135, Fig. 7); and as in *Labatia* among Sapotaceæ (see under that Family later in the present Volume, Part 11, p. 417). Sometimes in the form of finger-like processes (see 22, p. 132, Fig. 3). Gynæceum syncarpous. Carpels in two whorls, one enclosing the other as in Primulaceæ (*loc. cit.*, p. 407). The outer carpels form the wall of the ovary, the single style and the capitate stigma; those of the inner whorl the central column bearing the ovules. Number of carpels in the whorls variable. Those of the outer whorl sometimes corresponding with the number of vascular bundles (5 or 4 or more) entering the style. Fertile carpels as many as the sterile carpels or fewer. Ovules  $\infty$ . Fruit baccate or drupaceous, indehiscent.

The vascular bundles for the staminal whorls are carried out conjoined with the sepal midrib and petal midrib bundles, respectively. Those for the antesepalous staminodes, as in *Samolus* among Primulaceæ (see under that Family, *loc. cit.*, p. 407, Fig. 23), give rise to a basal pair of laterals which furnish the marginal venation system of the petal on each side. Furthermore, as is ordinarily the case when all, or part of a staminal member becomes sterile and assumes foliar form the midrib bundle gives rise to a branch system in the modified portion (see *e.g.* later under *Salvia* among Labiatæ, Part 12, p. 448).

## ILLUSTRATIVE TYPES

**Jacquinia armillaris** (Fig. 21; also 22, p. 131). A 'key' genus. Staminodes partly incorporated into the corolla as petaloid sectors alternating with the true petal lobes, and, in accord with their petaloid character, with a well-branched vascular system, thus corresponding in this Family with *Soldanella* among Primulaceæ (see under that Family, *loc. cit.*, p. 408, Fig. 24).



*Jacquinia armillaris*. Three petals from a corolla which has been cut in two longitudinally showing at the base the three trunk cords which furnish the petal midribs and stamen bundles, and alternating with them the bundles of two members of an antesealous staminal whorl now modified into petaloid staminodes. (In order to exhibit the whole of the vascular system the anthers have been removed.) (Reproduced from Fig. 5 in 22, p. 133.)

FIGURE 21.

**Clavija** spp. (e.g. *C. macrophylla*) (22, p. 131 and p. 133, Fig. 4). Staminodes in the form of sessile rounded cushions alternating with the petal lobes. The entering vascular bundle, in conformity with the external form, terminates in a brush-like group of short branches.



**Theophrasta.** Staminodes in the form of transversely elongated cushions seated on very short, broad, flattened bases which spring from the corolla near the base of the tube on the alternipetalous radii.

**Deherainia smaragdina** (22, p. 131 and p. 132, Figs. 2 and 3). Staminodes in the form of finger-like processes springing from the rim of the corolla tube and alternating with the petal lobes. The entering vascular bundle remains unbranched.

## 132. MYRSINACEÆ

Flower ♂ or more frequently through abortion unisexual, actinomorphic, hypogynous or more or less syngonous, tetramerous or pentamerous. K 4 C 4 or K 5 C 5. Petals conjoin below into a short tube or rarely entirely free. Antesepalous staminal whorl suppressed without outward trace but represented in some genera (*e.g. Ardisia*, see 22, p. 139), as in the bulk of Primulaceæ (see under that Family later in the present Volume, Part II, p. 406), by the corresponding vascular bundles. These bundles, when present, are carried out conjoined with the sepal midrib bundles, the antepetalous stamen bundles being similarly carried out conjoined with the petal midrib bundles as in Primulaceæ (see under that Family, *loc. cit.*, p. 406). Gynæceum similar in construction to that of Theophrastaceæ (see under that Family earlier in the present Volume, Part II, p. 401) and of Primulaceæ (*loc. cit.*, p. 407). Ovary unilocular with outer wall, style when present, and stigma(s) formed of a varying number of sterile carpels surrounding a central column of conjoined fertile carpels. Stigma lobes when distinct standing over the sterile carpels. Ovules seldom borne on the surface, more often sunk in the tissue of the central column, in contrast with the Primulaceæ in which the ovules are only exceptionally sunk (*Glaux*). Fruit generally stone-like.

Sepals with, or without, commissural marginal veins. The sterile carpel vascular bundles turn outwards from the residual central cylinder in the hypogynous types (*e.g. Ardisia, Myrsine*) and are detached from the inner face of the perianth-stamen cords and turn inwards in the syngonous forms (*e.g. Mæsa*). In both circumstances a ring of numerous vascular strands, showing no obvious relation to the primary radii, affords no certain clue to the number of sterile carpels which they serve. This number is indicated when the stigmas are distinct by the number of lobes, and in types with a style by the number

of vascular bundles entering the style base. Owing to the absence of a core of parenchyma in the basal region of the central column of the ovary, the vascular bundles of the fertile carpels form a continuous complex, so that they also give no clear index of the corresponding number of fertile carpels.

### ILLUSTRATIVE TYPES

**Ardisia spp.** Flowers ♂ or polygamous and diœcious, hypogynous. The longer or shorter style with punctiform or discoid stigma. Ovules sunk in the central column. Fruit one-seeded.

Sepals with commissural marginal veins. Antesepalous staminal whorl represented by the corresponding vascular bundles which, in accord with the shortness of the corolla tube, bifurcate immediately after separation from the sepal midrib bundles, the two forks giving rise, respectively, to the marginal venation system of the petal on either side, as in *Primulaceæ* (see under that Family, *loc. cit.*, p. 407).

**Myrsine.** Flowers polygamous and diœcious, hypogynous, 4- or 5-, more rarely 6- or 7-merous. The longer or shorter style with simple or lappeted stigma. Ovules sunk in the central column. Fruit one-seeded.

Sepals generally without commissural marginal veins. Antesepalous stamen bundles wanting.

**Mæsa.** Flowers ♂ or unisexual through abortion, more or less syngonous. Style short. Stigma lobed. Ovules not sunk in the central column but projecting from the surface. Fruit many-seeded.

Sepals generally with commissural marginal veins. Antesepalous stamen bundles wanting.

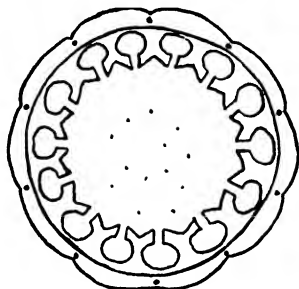
## 133. PRIMULACEÆ

Flower ♂, hypogynous or very exceptionally slightly syngonous (*Samolus*), actinomorphic or very rarely zygomorphic (*Coris*), often dimorphic, isomerous throughout or with a pleiomerous, rarely with an oligomerous gynæceum (e.g. *Glaux*) (3†, 17†, 22†). In general K 5 C 5 or rarely 0 (*Glaux*) A 5, rarely attaining separate morphological form (as in *Samolus* in which the filaments are without anthers and *Soldanella* in which, in the form of petaloid sectors, they are incorporated in the corolla) usually represented only by their vascular bundles, + 5 G 5 or up to 10 or fewer (*Glaux*), sterile + 5 or up to 10 or fewer (*Glaux*), fertile, forming a central column completely enclosed by the outer whorl (see Fig. 22). Ovary unilocular. Style single, formed of the sterile carpels. Stigma capitate, entire. Ovules generally numerous, rarely few (e.g. *Glaux*), borne on the central column (= the free-central placentation of the traditional terminology, see 3, p. 154 and 17, p. 260). Fruit a capsule, opening above by apical teeth or less often by transverse dehiscence (pyxidium).

Sepals very generally with commissural marginal veins (17, pp. 260, 261, 264 and Figs. 62, 63, 65-67). Corolla generally with a non-vascular continuous or interrupted curtain-like outgrowth in the throat. The perianth and andrœcium, when pentamerous, are supplied by ten trunk cords.

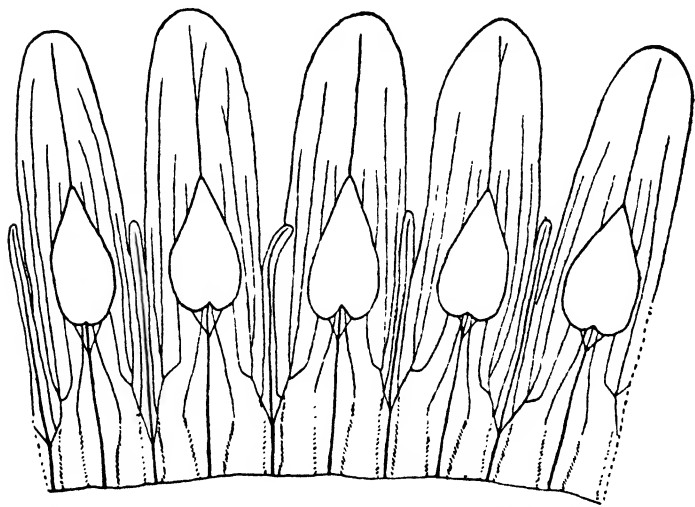
In *Samolus*, the five vascular cords on the sepal radii furnish the sepal midribs and the midrib bundles which pass into the antherless antesealous staminal filaments, and those lateral branches which enter, respectively, the petal on either side (see Fig. 23), and give rise to marginal systems. In *Soldanella*, the corresponding cords pass completely into the corolla, and give rise to the same vascular pattern of midrib and laterals as the petal components of the corresponding cords on the alternate radii (Fig. 24). In the other genera in which the antesealous staminal members do not attain morphological form, corresponding bundles arising in the

same way on the same radii similarly enter the corolla, and continue up the tube. As they approach the level at which the petals separate they fork. The two resulting strands pass, respectively, into the limb of the petal on either side



Garden *Polyanthus*. Transverse section of an ovary in which the wall is formed of ten carpels (indicated by the ten vascular bundles). (Reproduced from Fig. 66 in 3, p. 152.)

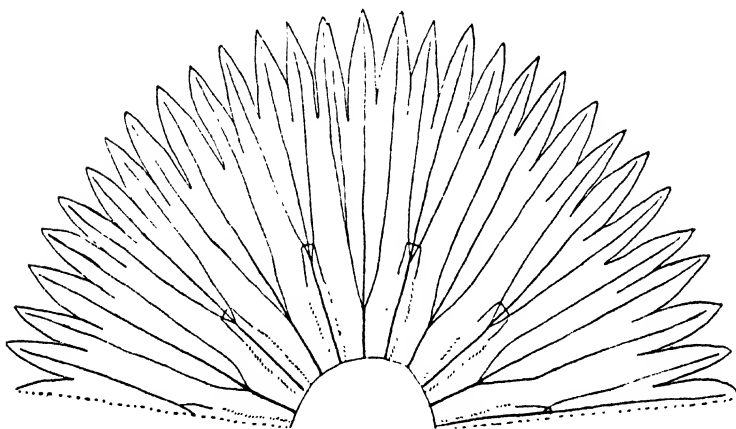
FIGURE 22.



*Samolus repens*. The corolla split longitudinally, viewed from the inner face. Alternating with the free petal segments the antherless filaments of the antesealous staminal whorl. (Reproduced from Fig. 1 in 22, p. 132.)

FIGURE 23.

and, as in *Samolus* (see above), give rise in the free portion of each petal to a marginal venation system, thus separate in origin from that derived from the petal midrib. The five trunk cords on the petal radii furnish the midribs of the petals and the bundles of the superposed, fertile stamens. Since the vascular bundles proper to the antesepalous whorl of the andrœcium arise as components of trunk cords the suppression of these antesepalous members, even were their bundles also to disappear, cannot affect the radial position of the succeeding whorl.

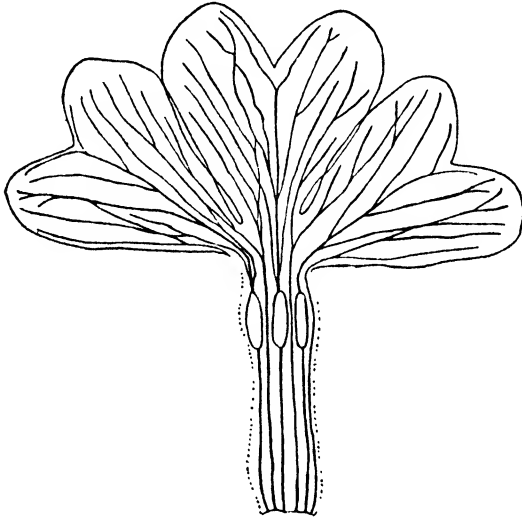


*Soldanella alpina*. The corolla split as in Fig. 23. The antesepalous staminal whorl is completely incorporated in the corolla. The individual members resemble the petals in form and in venation. (In order to expose the whole vascular system the anthers of the antepetalous stamens have been removed.) (Reproduced from Fig. 6 in 22, p. 135.)

FIGURE 24.

When the sterile carpel whorl, like the outer whorls, is pentamerous, the fertile carpel whorl is usually isomerous with it. When the carpels in the outer whorl are more numerous, those of the inner whorl, owing to lack of space, are generally fewer in number, and show no constant numerical relation to those of the outer whorl. When both whorls are pentamerous the outer carpels are antesepalous in some genera and antepetalous in others. The cause of this variability is not wholly clear. It may be connected with the fact that the midrib bundles of the sterile carpels do not turn outwards from the central vascular cylinder, but are detached from the inner face of the cylinder (which enlarges at the flower base) and

at first turn inwards. It appears that in these circumstances some additional, and as yet undetermined, interrelation must affect radial position, apart from those which ordinarily come into play when the course of the midrib bundles of the whorls is from the outset centrifugal.



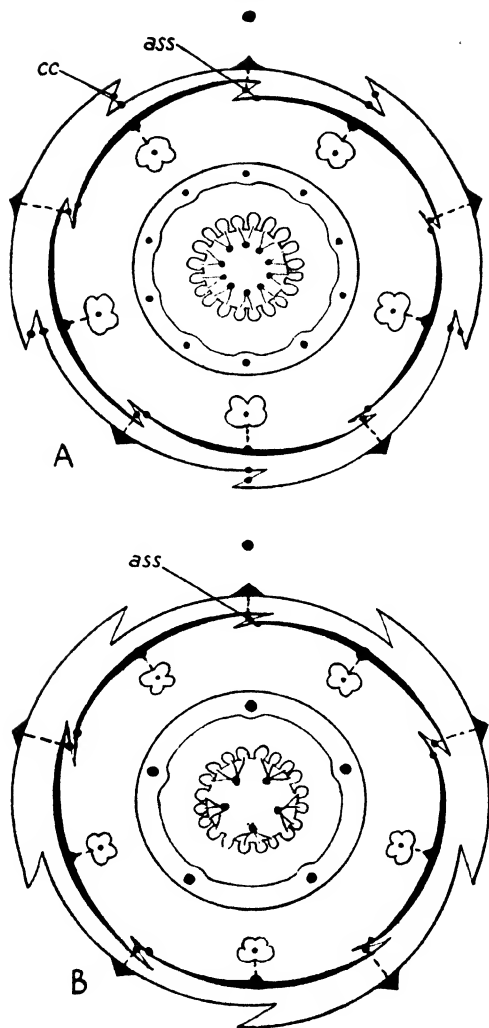
*Primula farinosa*. Three petals showing the scheme of venation typical of the genera in the Family in which the antesealous staminal whorl no longer attains separate morphological form. (Reproduced from Fig. 10 in 22, p. 138.)

FIGURE 25.

When the fruit dehisces by apical teeth, splitting occurs in line with the sterile carpel midribs, hence the resulting teeth do not correspond with individual whole carpels. A similar dehiscence by teeth in the mid-line of the carpels occurs in some Caryophyllaceæ, where also the resulting teeth do not correspond with single carpels (see Vol. I, Part 4, pp. 101, 102).

#### ILLUSTRATIVE TYPES

\**Primula acaulis* (Primrose). Antesealous stamens represented only by their vascular bundles (as in Fig. 25).

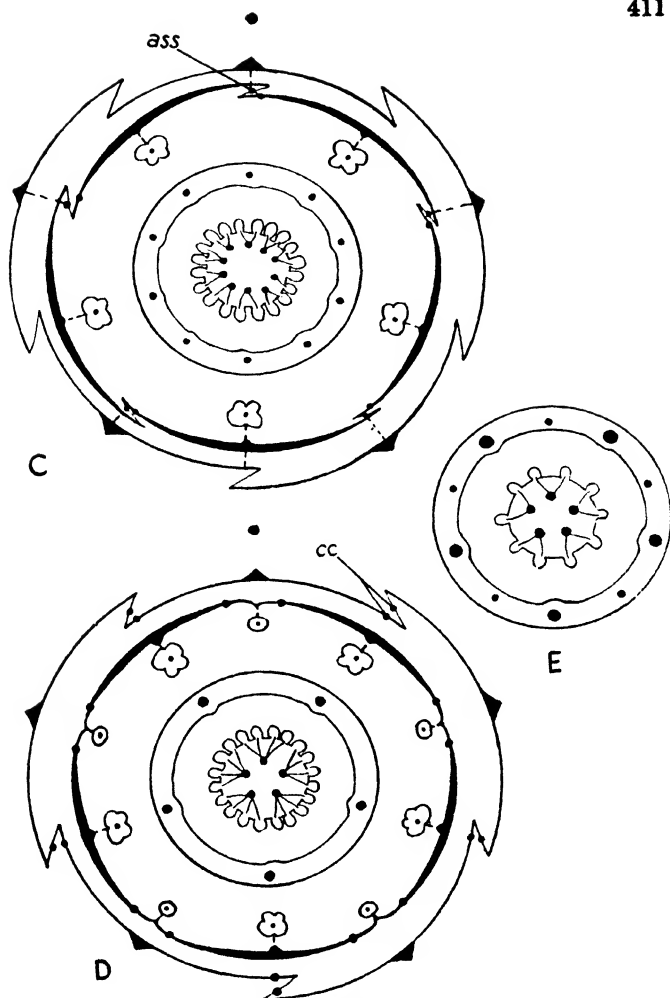


A. *Primula* type. Calyx with commissural marginal veins. The antesealous stamen bundles furnish the marginal veins of the free petal segments. G 10 + 10.  
 B. *P. floribunda*. Calyx without commissural marginal veins. Androecium as in A. G 5 + 5.

FIGURE 26 A, B.

(Figs. E, G, from 17, p. 281, improved.)





C. *Garden Polyanthus*. Calyx and androecium as in B. G 10 + 10.  
 D. *Samolus repens*. Calyx with commissural marginal veins. Antesepalous stamens present as staminodes with the corresponding vascular bundles. Lateral branches of the staminode bundles furnish the marginal veins of the free petal segments. G 5 + 5.  
 E. *Anagallis arvensis*. G 10 (5 with strong, 5 with weak bundles) + 5.  
 a s antesepalous stamen bundles which give rise to the marginal venation of the petals. c c commissural marginal veins of the sepals.

FIGURE 26 C, D, E.

(Figs. F, H, I, from 17, p. 281, improved.)

Sterile carpels and fruit teeth frequently 10 (as in Fig. 22. See also 17, pp. 272, 273, Figs. 72-78, and pp. 278, 279, Figs. 79-88).

**\*P. farinosa** (Bird's-eye Primrose) (see Fig. 25), **P. denticulata**. Andræcium as in *P. acaulis*. Sterile carpels and fruit teeth frequently 5 and then antesepalous.

**\*Samolus** (see Fig. 23; also 17, pp. 262, 263, Figs. 57-64). A 'key' genus. Antesepalous stamen whorl present in the form of staminodes. Sterile carpels when 5 antepetalous.

**Soldanella** (see Fig. 24; also 22, pp. 134-136, with Fig. 7). A 'key' genus. Antesepalous stamen whorl modified into petal-like structures incorporated in the corolla.

**\*Anagallis arvensis** (Common Pimpernel, Poor Man's Weatherglass). (17, pp. 266, 267, Figs. 65-71, and p. 281.) Calyx, corolla and andræcium as in the *Primula* type (see above). Fruit a pyxidium.

The variations in the floral and vascular relations described in the preceding pages are represented diagrammatically in Fig. 26, A, B, C, D, E, in which the diagrams which appeared in 17, p. 281, are improved.

## 134. PLUMBAGINACEÆ

Flower ♂, actinomorphic, hypogynous, pentamerous. K 5 C 5 A 0 + 5 G 5, sterile + 1, or ? 5 reduced and consolidated into a central, at first undifferentiated, core. Antesepalous staminal whorl suppressed without trace, morphological or vascular. Ovary syncarpous, 5-angled, unilocular, with the outer wall and styles formed, as in the Primulaceæ (see under that Family earlier in the present Volume, Part II, p. 406), of the sterile carpels. Styles 5, distinct throughout or connate below for a longer or shorter distance. Stigmas generally filamentous. A single basal ovule is borne on the central core which corresponds with the central column in the primulaceous ovary (see under Primulaceæ, *loc. cit.*, p. 406), but which here comes to an end as the loculus comes into being. Fruit indehiscent, or opening by a transverse split above or by an irregular tear at the base.

Sepals with true lateral veins (*e.g.* *Statice*) or with commissural lateral veins which turn out independently from the central vascular cylinder, but are derived from a vascular complex on each petal radius which also furnishes a petal midrib (*e.g.* *Ceratostigma*). Petal midribs and antepetalous stamen bundles, as in Primulaceæ (*loc. cit.*, p. 408), conjoined at first forming a single set of trunk cords, becoming disjoined later, consequently the fourth (sterile carpel) whorl is antesepalous. As the five sterile carpel bundles turn outwards, elements left behind on the intermediate radii become 'condensed' into a solid core from which the funicle bundle is eventually differentiated. It is thus difficult to determine whether this core should be regarded as corresponding to five potentially fertile carpels of which only one is functional or whether it should now definitely be looked upon as representing a single carpel. A similar problem is presented by other Families having a unilocular ovary and a solitary basal ovule, as *e.g.* Myricaceæ, Basellaceæ, Chenopodiaceæ, Amarantaceæ (see under these Families earlier in the present Volume, Part 9, p. 329, and Part 10, pp. 376, 360, 364, respectively). As the ovule develops the funicle becomes pressed sideways by the nucellus and comes to lie in an angle of the

loculus in line with a sterile carpel midrib, a position determined simply by space conditions and not indicative of the radius of origin.

### ILLUSTRATIVE TYPES

**\**Armeria vulgaris*** (Thrift). Inflorescence a dense globular head terminating an unbranched leafless stem and surrounded by coloured scarious bracts. Petals free almost to the base. Staminal filaments becoming free from the corolla as the petals separate. Styles free. Fruit opening at the base by a ring-shaped tear.

**\**Statice Limonium*** (Sea Lavender). Flowers in 3-flowered spikelets on one-sided spikes in dichotomously or trichotomously branched panicles. Petals united for a short distance at the base. Staminal filaments becoming free from the corolla at the level at which the petals separate. Styles free. Fruit indehiscent.

***Ceratostigma* spp.** Staminal filaments becoming free half-way up the corolla. Styles connate.

***Plumbago* spp.** Staminal filaments free from the corolla. Styles connate below.

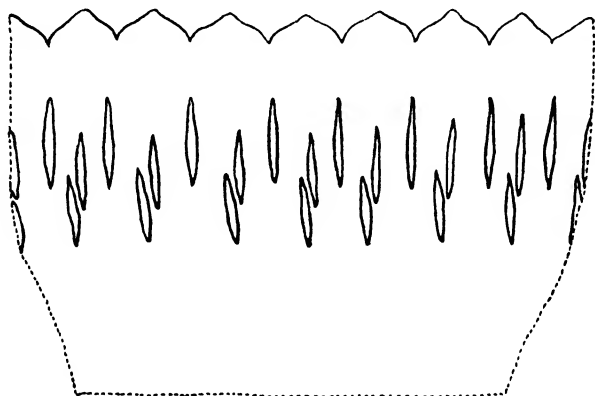
## 135. SAPOTACEÆ

Flowers generally ♂, less often through abortion polygamous, hypogynous, actinomorphic. Sepals generally 4, 6 or 8, 2-seriate, as frequently in types in other Families with K 4 or K 6 (for other instances see those cited earlier in the present volume under Lauraceæ, Part 10, p. 383); seldom 5 and 1-seriate; still more rarely 7 or up to 12 and acyclic. Petals generally 1-seriate, being then equal in number to the total number of sepals and alternating with them as a whole (*i.e.* as one whorl); rarely twice the number of sepals, or more or less numerous (*e.g.* *Vitellaria spp.*). The andrœcium generally in two whorls, isomerous, respectively, with the 2-seriate calyx and with the corolla in genera where these two perianth whorls are also isomerous, the antesepalous members being staminodal; in one whorl through suppression of the antesepalous members in genera with a 1-seriate calyx, and then usually isomerous with the petals and superposed upon them, rarely fewer through abortion; sometimes three times as many as the petals but then never in three alternating whorls. The 3-tier arrangement giving rise to the illusory appearance of three whorls arises from the different levels at which the twin stamens on each petal radius (due to duplication of each antepetalous member) become free from the corolla as in *Bassia (Illipe) latifolia* (see Fig. 27), in which a single tier of antesepalous stamens becoming free at a higher level alternates with the petals, and two tiers becoming free at lower levels are superposed on the petals and represent a duplicated antepetalous whorl (24, p. 139).

Sepals with true lateral veins arising simultaneously with the midrib bundles from the central cylinder. The vascular bundles for the antesepalous stamens turn out from the central cylinder independently; those for the antepetalous

members are derived from the same, sometimes ill-defined, vascular units as the petal midribs, a bundle being given off on each side of each of these units at a different level as they break up into the petal and staminal components.

Similar duplication of the antepetalous staminal whorl associated with a corresponding division of the staminal



*Bassia (Illipe) latifolia*. Corolla and androecium from a flower with C 8 A 8 + 8<sub>2</sub>. Alternipetalous (antesepalous) stamens single, antepetalous stamens duplicated.

FIGURE 27.

component of the petal stamen, trunk cords occurs in *Monsonia* and *Sarcocaulon* among Geraniaceæ (see under that Family in Vol. I, Part 3, p. 72), though in these latter genera the break-up of the petal-stamen vascular unit takes place farther away from the central cylinder. (For other instances see those cited earlier in the present Volume under Hamamelidaceæ, Part 5, p. 163). Staminodal modification of the antesepalous stamen whorl varies in degree. In some genera, *e.g.* *Labatia*, these members may be incorporated into the corolla as recognisably distinct petaloid sectors alternating with the true petals, as in *Jacquinia* among Theophrastaceæ and in *Soldanella* among Primulaceæ (see under these Families earlier in the present Volume, Part 11, pp. 402 and 408, respectively; also 22, pp. 129–137 with Fig. 7). In other genera, *e.g.* *Lucuma*, *Vitellaria* and *Monothea* (*Edgeworthia*, *Reptonia*), they form antherless filaments, as in *Samolus* (Primulaceæ) (see under the latter Family, *loc. cit.*; also 22, *loc. cit.*).

Gynæceum syncarpous. Carpels in two isomerous whorls, the outer sterile, the inner fertile, those of each whorl being generally isomerous with the petals, sometimes twice as many; the ovary, accordingly, with as many loculi as petals or with twice as many. Doubling of the number of carpels in the whorls and of the loculi is due to a change of rhythm, a whorl of sterile carpels being developed on both sets of construction radii, and a whorl of fertile carpels on a wholly new set of intermediate radii. Ovules solitary in each loculus or rarely two in an individual loculus and then generally in the absence of an ovule in a neighbouring loculus. Style single with a 4- to 12-rayed stylar canal in accord with the number of fertile carpels and of loculi. Stigma terminal, punctiform, with as many lobes as sterile carpels and with the lobes centred over these carpels. Margin of the stigma entire when the canal rays form a single central opening (*e.g.* species of *Palaquium* and *Mimusops*, *Achras Sapota*), sinuous when the rays, remaining distinct, open outwards through median radial splitting of the fertile carpels at the apex (*e.g.* *Chrysophyllum Cainita*). Fruit a berry.

### ILLUSTRATIVE TYPES

**Chrysophyllum maytenoides.** K 5 C 5 A 0 + 5 G 5 sterile + 5 fertile.

**C. Cainita.** K 5 C 5 A 0 + 5 G 10 sterile + 10 fertile.

In the absence of sufficient data concerning the vascular scheme the expression A 0 + 5 in the above descriptions must be taken to imply simply loss of morphological form in the antesealous whorl.

**Sideroxylon spp.** K 5 C 5 A 5 staminodal, becoming free from the inner face of the corolla + 5 G 5 sterile + 5 fertile.

**Labatia.** A 'key' genus K 4 (2-seriate) C 4 A 4 staminodal, incorporated into the corolla, as in *Jacquinia armillaris* among Theophrastaceæ and *Soldanella* among Primulaceæ

(see above under the account of the Family) + 4 G 4 sterile + 4 fertile.

**Bassia (Illipe) latifolia** (Fig. 27). K 4 (2-seriate) C 4 + 4 A 8 + 8, G 8 sterile + 8 fertile.

**Palaquium (Isonandra) Gutta** (Gutta-Percha tree). K 4 (2-seriate) C 4 A 4 + 4 G 4 sterile + 4 fertile.

Other species. K 6 (2-seriate) C 6 A 6 + 6 G 12 sterile + 12 fertile.

Other species. K 6 (2-seriate) C 6 A 6 + 6, G 12 sterile + 12 fertile.

**Achras Sapota.** K 6 (2-seriate) C 6 A 6 staminodal + 6 G 12 sterile + 12 fertile.

**Mimusops Elengi.** K 8 (2-seriate) C 8 A 8 staminodal + 8 G 8 sterile + 8 fertile.

[N.B.—The floral formulæ cited above are characteristic but it should be understood that they are not invariable, the number of members in the whorls often varying from individual to individual or even from flower to flower.]



## 136. EBENACEÆ

Flowers generally unisexual and diœcious with rudiments of the non-functional sex, less often ♂ or polygamous, actinomorphic, hypogynous. Calyx, corolla and andrœcium 5-7-merous. Stamens in one or two whorls, the antepetalous whorl being sometimes duplicated, sometimes suppressed. Ovary syncarpous, multilocular, sometimes with as many loculi as fertile carpels through union of these carpels in the centre, sometimes with twice as many through the extension of the sterile as well as the fertile carpels to the centre. Carpels in each whorl 2-16; sterile carpel whorl when isomerous with the perianth whorls antepetalous (often erroneously described as antesepalous). Ovules 1 or 2 in each loculus, pendulous. Styles more or less distinct, as many as the sterile carpels and centred over these carpels, or completely connate. Stigmas entire or 2-lobed. Fruit fleshy or leathery, rarely dehiscing by valves.

Those isomerous types having twice as many loculi as members in any one whorl present a resemblance to similar types in Sapotaceæ which also have twice as many loculi as sepals or petals. But the likeness is only superficial, the doubling of the loculi being brought about in a different manner in the two Families. For in isomerous Ebenaceæ this doubling is not the result of a change in the ground-plan but is due to the morphological character of the sterile carpels, which like the fertile carpels, form complete partitions. Whereas in Sapotaceæ it follows from an alteration in the rhythm, not from the sterile carpels being of unusual form. This change in rhythm results in the development of an outer whorl of sterile carpels on both sets of construction radii and of an inner whorl of a corresponding number of fertile carpels on a

wholly new set of intermediate radii. While isomerous Sapotaceæ are thus represented by  $K\ n\ C\ n\ A\ n + n\ G\ 2\ n + 2\ n$  with  $2\ n$  loculi similar types among Ebenaceæ are represented by  $K\ n\ C\ n\ A\ n + n\ G\ n + n$  with  $2\ n$  loculi. Similar doubling of the loculi is met with in *Linum*, which offers an almost exact parallel with Ebenaceæ, the chief difference being that in Ebenaceæ this condition is maintained to near the top of the ovary, whereas in *Linum* it is only present in the lower region of the ovary, the sterile carpels in the upper region being withdrawn from the centre into the ovary wall (see under Linaceæ in Vol. I, Part 3, p. 77; also 3, p. 148, Figs. 55-58).

The vascular bundles for the antesepalous stamen whorl turn out from the central cylinder independently, those for the antepetalous whorl are carried out conjoined at first with the petal midrib bundles, hence suppression of this latter staminal whorl in some types does not affect the radial position of the members of the succeeding whorl, the sterile carpels being always antepetalous. Duplication of the antepetalous staminal whorl occurs when the corresponding petal-stamen trunk cord breaks up in such a way that a staminal component is left on each side of the petal midrib in place of a single staminal component in line with the petal midrib.

## ILLUSTRATIVE TYPES

**Diospyros Kaki.** ♂ Flower.  $K\ 4\ C\ 4\ A$  through duplication often  $16\ G$  (if present) rudimentary. ♀ Flower.  $K\ 4\ C\ 4\ A\ 4 + 4$ , all staminodal  $G\ 4$ , sterile  $+ 4$ , fertile. Ovary 8-locular since the sterile as well as the fertile carpels extend to the centre, becoming 4-locular at the summit as the sterile carpels become withdrawn into the outer wall. Style single with a four-rayed stylar canal, each ray standing in line with a sterile carpel (since each ray represents the line of closure of the two loculi bordering each sterile carpel after the fusion of these two loculi into a single cavity when the intervening sterile carpel ceases to extend to the centre). Stigmas 4, bilobed,

standing over the sterile carpels, arising through the median radial splitting of the fertile carpels, each corresponding to a sterile carpel bordered on each side by half the adjacent fertile carpel on that side ( $\frac{1}{2}$  1  $\frac{1}{2}$ ).

**Royena spp.** ♀ Flower. K 5 C 5 A 5 + 5, all staminodal G 5, sterile + 5, fertile. Ovary 10-locular, becoming 5-locular at the summit. Style single below with a five-rayed styler canal, shortly separating into five filaments, each of  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels through median radial splitting of the fertile carpels. Otherwise as in *Diospyros Kaki* (see above).

## 137. STYRACACEÆ

Flower ♂, actinomorphic, syngonous or hypogynous, the basic ground-plan consisting of six isomeric 4- or 5-merous whorls ( $K\ n\ C\ n\ A\ n + n\ G\ n$ , sterile +  $n$ , fertile,  $n$  being 4 or 5), but sometimes deviating from this construction through multiplication, rarely through suppression, of the antepetalous stamens; or through reduction, after a process of vascular reconstruction, of the number of carpels. Gynæceum syncarpous. Ovary with as many loculi as fertile carpels through union of these carpels in the centre, but often becoming unilocular above as they no longer extend to the centre. Loculi antesealous. Ovules 1-few in each loculus. Style single. Stigma terminal, capitate or lobed, the lobes being centred over the sterile carpels. Fruit dry, indehiscent or dehiscent at the top into valves, or drupaceous.

The vascular bundles of the two whorls of stamens do not originate independently, but arise from the same units as the sepal and petal midrib bundles, respectively; hence the antesealous position of the loculi in isomeric types even when six-whorled (see Vol. I, Introduction, p. 8).

## ILLUSTRATIVE TYPES

**Halesia diptera** (Snowdrop-tree). Flower syngonous.  $K\ 4\ C\ 4\ A\ 4 + 4_{1-2}$ ,  $G\ 4$ , sterile, antesealous + 4, fertile, antepetalous or  $K\ 5\ C\ 5\ A\ 5 + 5_{1-2}$ ,  $G\ 3-5$ , sterile + 3-5, fertile. In tetramerous flowers the sepals occupy the angles, the petals the flat sides of the four-sided outline. Stamens springing from the base of the corolla tube and then appearing to stand in a single ring. Ovary with as many loculi as fertile carpels but becoming unilocular above. Style filamentous. Stigma lobes small, centred over the sterile carpels. Fruit dry, indehiscent.

Sepals with commissural marginal veins. The vascular bundles of the antesealous stamens originate in the centre,

those for the antepetalous stamens are detached from the trunk cords on the petal radii which also furnish the petal midrib bundles. A single staminal bundle may be detached from the inner face of each of these trunk cords or two bundles may be given off laterally, one on each side, from one or all of these cords. Since the break-up of these trunk cords varies in this way, not only from flower to flower, but also from one radius to another in the same flower, the total of stamens in the tetramerous flower may be any number from 8 to 12, and in the pentamerous flower from 10 to 15. And since this division of the antepetalous staminal vascular components, when it occurs, takes place outside the residual vascular ring serving the gynæceum, and hence after the determinate phase has been reached, these antepetalous pairs of stamens are whole stamens. For the reverse case in which division of the staminal vascular component takes place before these components have turned out from the central vascular ring, and, therefore, before the determinate phase has been reached, with the result that the pairs of stamens which these bundles serve are half-stamens, see Vol. I, under *Fumarioideæ* among *Papaveraceæ*, Part 2, p. 48, and under *Malvaceæ*, Part 4, p. 106. For other examples in which there is duplication with the formation of whole stamens, see in the present Volume under *Sapotaceæ*, Part II, p. 415, and for other instances under *Hamamelidaceæ*, Part 5, p. 163.

In the region of the ovary the vascular system of the sterile carpels consists of a number of bundles which in the style are reduced to the midribs. Fertile carpels without midrib bundles, but with the twin placental bundles prolonged separately into the style which thus receives twelve bundles in the tetramerous type, fifteen bundles when the gynæceum is pentamerous. (For a similar unusual prolongation of the placental bundles up the style, see earlier in the present Volume under *Pirola* (*Pirolaceæ*), Part II, p. 392.) As the single style gives rise above to the separate stigma-bearing branches through median radial splitting of the fertile carpels, each branch receives a sterile carpel midrib and one placental strand from the neighbouring fertile carpel on each side, and hence corresponds to  $\frac{1}{2} \times 1 \frac{1}{2}$  carpels.

**Styrax.** Flower hypogynous or more or less syngonous. K 5 C 5 A 5 + 5 G 3 (or 4), sterile + 3 (or 4), fertile. Ovary trilocular (or quadrilocular) below, becoming unilocular above as the fertile carpels no longer extend to the centre. Style single. Stigma capitate or slightly 3- (or 4-) lobed, with the lobes centred over the sterile carpels. Fruit dry or drupaceous.

The vascular bundles of perianth and andræcium are derived

from ten trunk cords, those on the sepal radii furnish the sepal midribs and antesepalous stamen bundles, those on the petal radii the commissural marginal veins of the sepals, petal midribs and antepetalous stamen bundles. The reduced number of carpel bundles are organised after a process of reconstruction in the residual central cylinder.

Ovaries with the ground-plan  $G 4 + 4$  are nevertheless sometimes trilocular owing to the failure of one of the fertile carpels to develop normally in the radial direction, so that unlike the other three fertile members, it does not project into the ovary cavity and does not form a placenta or bear ovules, but merely forms the outer wall of the ovary on that radius. The presence of this imperfectly developed carpel in such ovaries may be inferred from the double size of the loculus on this radius (necessarily resulting from this conformation) as compared with that of the other two, but is definitely established by the occurrence in the ovary wall of the corresponding vascular bundle and by the four-rayed outline of the styler canal when the other three fertile carpels eventually assume the same morphological form as the carpel in question. For a like result in other types, due to failure in radial development of one member of the fertile carpel whorl and for the converse case of the production of a double-sized septum through failure in development of the intervening sterile carpel and loculus, see instances cited under *Deutzia* (*Saxifragaceæ*) earlier in the present Volume, Part 5, p. 151.

## Part 12

### Dicotyledons

Family	138.	Oleaceæ
„	139.	Gentianaceæ
„	140.	Apocynaceæ
„	141.	Asclepiadaceæ
„	142.	Convolvulaceæ
„	143.	Polemoniaceæ
„	144.	Hydrophyllaceæ
„	145.	Boraginaceæ
„	146.	Verbenaceæ
„	147.	Labiataæ
„	148.	Nolanaceæ
„	149.	Solanaceæ
„	150.	Scrophulariaceæ
„	151.	Lentibulariaceæ
„	152.	Orobanchaceæ
„	153.	Gesneriaceæ
„	154.	Bignoniaceæ
„	155.	Globulariaceæ
„	156.	Acanthaceæ
„	157.	Myoporaceæ
„	158.	Plantaginaceæ





## 138. OLEACEÆ

Flowers generally ♂, rarely unisexual or polygamous, hypogynous, actinomorphic. K 4, in two pairs (or up to 15 or more, or 0) C 4 (–6 or more or sometimes wanting) A 2 lateral, rarely median (or 3–5) G 2 alternating with the stamens when the andrœcium is dimerous, sterile + 2, fertile, rarely 4 + 4 (*Osmanthus* ♀). Ovary bilocular, rarely quadrilocular through union of the fertile carpels in the centre. Ovules generally 2 in each loculus. Style single. Stigma generally bilobed, with the lobes centred over the sterile carpels. Fruit a berry, or drupe, or capsule dehiscing loculicidally or rarely septicidally (*Fontanesia*), or winged and indehiscent.

### ILLUSTRATIVE TYPES

**Syringa** (Lilac). K 4, orthogonal, C 4, diagonal, A 2, lateral G 2, median, sterile + 2, lateral, fertile. Ovary bilocular. Stigma bilobed. Ovules 2 in each loculus, pendulous. Fruit a capsule dehiscing loculicidally.

**Forsythia**. Flower as in *Syringa* (see above).

Owing to the comparatively large size of the flower the vascular ground-plan is particularly easily observed. Sepals with true lateral veins.

**\*Ligustrum** (Privet). Flower as in *Syringa* (see above). Fruit a berry.

**\*Fraxinus**. Flowers polygamous or diœcious. Fruit one-seeded, winged indehiscent.

**\*F. excelsior** (Common Ash). ♀ Flower. K 0 C 0 A 2 G 2, median, sterile + 2 lateral, fertile.

**F. Ornus** (Manna Ash). ♀ Flower. K 4 C 4 A 2 G 2, median, sterile + 2, lateral, fertile.

## 139. GENTIANACEÆ

Flowers almost always ♂, actinomorphic and hypogynous, rarely slightly syngonous (*Menyanthes* spp., *Limnanthemum* spp.) or unisexual and dioecious (*Swertia*), or slightly zygomorphic (*Canscora*). Perianth and andrœcium generally 5- or 4-merous (K 5 C 5 A 5 or K 4 C 4 A 4), sometimes 6- to 8-merous (*Chlora*), exceptionally, up to 9-merous (some *Gentiana* spp.) or even up to 12-merous (*Sabbatia*). A glandular non-vascular disc of varied form usually present at the base of the ovary. Ovary generally unilocular, the fertile carpels projecting in varying degree into the locus but not reaching the centre; rarely bilocular (*Exacum*, *Sebæa*). Carpels commonly 4, 2 sterile, 2 fertile (e.g. *Chlora*, *Erythræa*, *Gentiana* spp., *Menyanthes*, *Villarsia*, *Limnanthemum*, *Exacum*, *Sebæa*, *Chironia*, *Eustoma*, *Pleurogyne*); in individual flowers sometimes 6, 3 sterile, 3 fertile (e.g. *Menyanthes*, *Limnanthemum*). In some species of *Gentiana* sterile carpels 2 with fertile carpels (?) > 2 (see below under Illustrative Types). Style single. Stigmas generally 2 standing over the sterile carpels.

Exceptionally, the conducting tissue in the style may come to the surface on each side below the summit, and at these situations give rise to additional separate tufts or tracts of stigmatic papillæ in line with the conducting tracts in the ovary wall (*Sebæa*). Or the two separate tracts of this tissue in the wall of the unilocular ovary may exceptionally extend to the surface along the whole length of the ovary and give rise to two longitudinal bands of stigmatic papillæ continuous with the terminal sessile stigma in a styleless gynæceum (*Pleurogyne*). (See also under *Gentiana* and *Chlora* among Illustrative Types.)

Ovules in several rows, sometimes covering almost the whole inner surface of the ovary wall (e.g. *Gentiana* spp.). Fruit a capsule, dehiscing into two valves, or splitting

irregularly at the summit, or indehiscent; very rarely baccate (*Chironia*).

The vascular bundles for the stamens may turn out from the central cylinder independently (most genera), or they may be components of the trunk cords on the sepal radii from which they separate later after the carpel components (if any) have been detached (*Menyanthes*, *Villarsia*, *Limnanthemum*).

### ILLUSTRATIVE TYPES

**\**Menyanthes trifoliata*** (Buckbean). Flower slightly syngonous. K 5 C 5 A 5 G 4, 2 sterile, 2 fertile; in individual flowers G 6, 3 sterile, 3 fertile. Style club-shaped at the summit ending in 2 (or 3) truncate stigmatic lobes. Fruit a capsule, indehiscent or tearing irregularly at the summit.

The vascular ground-plan shows slight 'condensation' in that not all the ten primary trunk cords from which the midribs of the several whorls are derived turn outwards singly, two neighbouring cords sometimes arising conjoined together for a short distance and then separating to take up their positions on their proper radii. The placental bundles of the fertile carpels are the first to be delimited, being detached from the inner face of a corresponding number of the single or combined trunk cords as these cords turn out horizontally. Shortly afterwards the sterile carpel midribs are similarly detached from a corresponding number of the now separate trunk cords. Later, each of the five cords on the sepal radii gives rise to a sepal midrib and an antesepalous stamen bundle; each of those on the alternate radii becomes a petal midrib. When  $G = 4$  the two sterile carpel midribs are detached from one of the cords on the sepal radii and from the cord on the opposite petal radius. When  $G = 6$  the spacing of the carpel bundles is inevitably unequal. As ordinarily when reduction occurs in the gynæceum and the carpel bundles originate as components of the primary trunk cords restriction of the bundles of one set of carpels to one set of radii is abandoned. In this way the spacing is as nearly equal as the conditions allow. At the top of the ovary the fertile carpel bundles divide in two. Both the resulting pairs of bundles and the sterile carpel midribs continue into the style, but only the sterile carpel bundles persist into the stigmas, the others coming to an end at indeterminate levels.

***Villarsia parnassifolia***. Flower hypogynous. K 5 C 5

A 5 G 4 or occasionally 6, as in *Menyanthes* (see above). Style ending in a funnel-shaped stigma of 2 (or 3) broad, alternating with 2 (or 3) narrow lappets corresponding with the number of carpels.

The style receives the vascular systems of both the sterile and the fertile carpels, both sets of bundles extending to the stigma level.

**\**Limnanthemum nymphæoides*.** Flower slightly syn-gonous. K 5 C 5 A 5 (sometimes K 4 C 4 A 4) G 4, 2 sterile, 2 fertile. Stigmatic papillæ forming a continuous sinuous crest, which is reflexed over the sterile carpels, inflexed over the fertile members.

When the outer whorls are tetramerous the bundles for the four carpels are detached from the four cords on the sepal radii which also furnish the sepal midribs and stamen bundles. The style receives only the two midrib bundles of the sterile carpels.

**\**Gentiana*.** A large genus showing considerable variation in the anatomy of the gynæceum, the analysis of which in many species presents some difficulty. Outer whorls 5- or 4-merous, rarely 6- or 7-merous. Ovary with a longer or shorter stipe surrounded by a non-vascular 5- or 4-lappeted disc. The stamen bundles turn out from the central cylinder independently. Sterile carpels always 2. Fertile carpels 2 or (?) more (see below). Style very variable in length. Stigmas 2, short and broad, or long, slender and recurved, standing over the sterile carpels. Only the sterile carpel midribs, as a rule, prolonged into the style. Fruit a capsule dehiscing into two valves.

**\**G. campestris*** (Field Gentian). K 4 C 4 A 4 G 4, 2 sterile, 2 fertile, the fertile members not projecting into the loculus. Fruit dehiscing by radial splitting of the fertile carpels.

Residual vascular elements for the gynæceum remain disposed on four radii. These four units become organised directly into the two sterile carpel midribs and the two bundles of the fertile carpels. This reduction of the residual vascular tissue serving the gynæceum to four

bundles corresponding with the four carpels represents the simplest type of gynæceal construction and presents no difficulty.

**G. spp.** with a gynæceum of more complex structure (*e.g.* **cruciata** (see 3, pp. 154, 155 and p. 152, Fig. 67), **asclepiadea**, **decumbens**, **Saponaria**, **tianschanica gelida**, **phogifolia**, **hascombensis** (a garden form)). Outer whorls (K, C, A) pentamerous or tetramerous.

The residual vascular tissue serving the gynæceum consists of 6–20 or more bundles arranged in a ring round the central parenchyma which gives place to the loculus as the longer or shorter stipe passes into the expanded region of the ovary. These bundles (sometimes reduced in number in this latter region through fusion) continue to the top of the ovary. Two standing opposite to one another become the midribs of two sterile carpels. Of the others all may bear ovules so that where these bundles are numerous almost the whole inner surface of the ovary wall may be covered with ovules. These fertile bundles are very generally of unequal size and unequally spaced, and some at least appear to be of the concentric type in contrast with the sterile midribs which are dorsiventral. In the upper portion of the ovary two tracts of conducting tissue make their appearance on the inner surface of the ovary wall. These tracts are situated in a plane which cuts the plane of the sterile carpel midribs obliquely, hence they do not divide the side walls of the ovary into two equal portions. As the loculus closes the two tracts fuse and continue upwards as the core of the style to give rise at its summit to the stigmatic papillæ. These tracts indicate the lines of dehiscence in the fruit. In some species (*e.g.* *G. asclepiadea*) the ovary wall, even in the flowering stage, is cleft towards the top from without inwards as far as this tissue. Stigmatic papillæ derived from this tissue line these narrow clefts, but do not extend further to the exterior.

The separate origin of the several fertile bundles which often occupy every radius between the sterile carpel midribs makes it difficult to regard the whole number as constituting the much-branched systems of two fertile carpels comparable with the two fertile carpels in such species as *G. campestris*. On the other hand, owing to the often unequal size and spacing of these bundles, it seems no less difficult to determine whether all, or if not all how many, correspond to individual fertile carpels. For example, in a flower of *G. Saponaria*, with K 4 C 4 A 4, ten residual bundles about equally spaced and of approximately equal size were present at the base of the stipe. These bundles still retained their individuality at

A 5 G 4 or occasionally 6, as in *Menyanthes* (see above). Style ending in a funnel-shaped stigma of 2 (or 3) broad, alternating with 2 (or 3) narrow lappets corresponding with the number of carpels.

The style receives the vascular systems of both the sterile and the fertile carpels, both sets of bundles extending to the stigma level.

**\**Limnanthemum nymphæoides*.** Flower slightly syngonous. K 5 C 5 A 5 (sometimes K 4 C 4 A 4) G 4, 2 sterile, 2 fertile. Stigmatic papillæ forming a continuous sinuous crest, which is reflexed over the sterile carpels, inflexed over the fertile members.

When the outer whorls are tetramerous the bundles for the four carpels are detached from the four cords on the sepal radii which also furnish the sepal midribs and stamen bundles. The style receives only the two midrib bundles of the sterile carpels.

**\**Gentiana*.** A large genus showing considerable variation in the anatomy of the gynæceum, the analysis of which in many species presents some difficulty. Outer whorls 5- or 4-merous, rarely 6- or 7-merous. Ovary with a longer or shorter stipe surrounded by a non-vascular 5- or 4-lappeted disc. The stamen bundles turn out from the central cylinder independently. Sterile carpels always 2. Fertile carpels 2 or (?) more (see below). Style very variable in length. Stigmas 2, short and broad, or long, slender and recurved, standing over the sterile carpels. Only the sterile carpel midribs, as a rule, prolonged into the style. Fruit a capsule dehiscing into two valves.

**\**G. campestris*** (Field Gentian). K 4 C 4 A 4 G 4, 2 sterile, 2 fertile, the fertile members not projecting into the loculus. Fruit dehiscing by radial splitting of the fertile carpels.

Residual vascular elements for the gynæceum remain disposed on four radii. These four units become organised directly into the two sterile carpel midribs and the two bundles of the fertile carpels. This reduction of the residual vascular tissue serving the gynæceum to four

bundles corresponding with the four carpels represents the simplest type of gynæceal construction and presents no difficulty.

**G. spp.** with a gynæceum of more complex structure (*e.g.* **cruciata** (see 3, pp. 154, 155 and p. 152, Fig. 67), **asclepiadea**, **decumbens**, **Saponaria**, **tianschanica gelida**, **phogifolia**, **hascombensis** (a garden form)). Outer whorls (K, C, A) pentamerous or tetramerous.

The residual vascular tissue serving the gynæceum consists of 6–20 or more bundles arranged in a ring round the central parenchyma which gives place to the loculus as the longer or shorter stipe passes into the expanded region of the ovary. These bundles (sometimes reduced in number in this latter region through fusion) continue to the top of the ovary. Two standing opposite to one another become the midribs of two sterile carpels. Of the others all may bear ovules so that where these bundles are numerous almost the whole inner surface of the ovary wall may be covered with ovules. These fertile bundles are very generally of unequal size and unequally spaced, and some at least appear to be of the concentric type in contrast with the sterile midribs which are dorsiventral. In the upper portion of the ovary two tracts of conducting tissue make their appearance on the inner surface of the ovary wall. These tracts are situated in a plane which cuts the plane of the sterile carpel midribs obliquely, hence they do not divide the side walls of the ovary into two equal portions. As the loculus closes the two tracts fuse and continue upwards as the core of the style to give rise at its summit to the stigmatic papillæ. These tracts indicate the lines of dehiscence in the fruit. In some species (*e.g.* *G. asclepiadea*) the ovary wall, even in the flowering stage, is cleft towards the top from without inwards as far as this tissue. Stigmatic papillæ derived from this tissue line these narrow clefts, but do not extend further to the exterior.

The separate origin of the several fertile bundles which often occupy every radius between the sterile carpel midribs makes it difficult to regard the whole number as constituting the much-branched systems of two fertile carpels comparable with the two fertile carpels in such species as *G. campestris*. On the other hand, owing to the often unequal size and spacing of these bundles, it seems no less difficult to determine whether all, or if not all how many, correspond to individual fertile carpels. For example, in a flower of *G. Saponaria*, with K 4 C 4 A 4, ten residual bundles about equally spaced and of approximately equal size were present at the base of the stipe. These bundles still retained their individuality at

the level of appearance of the loculus. Two opposite bundles as usual remained sterile, the others served the numerous rows of ovules. In view of these facts it seems most satisfactory to interpret the evidence as indicating that the vascular systems of more than two fertile carpels have persisted, that these systems are in process of reduction by 'condensation' or by loss, and that in this transition state it is not possible to determine the number of fertile carpels which these bundles represent. Similar 'condensation' of vascular strands, which originally served a full number of carpels into the bundles of a reduced number, occurs in other Families. It is characteristic of many Leguminosæ-Papilionatæ in which the bundles for the one sterile and one fertile carpel of the legume are organised from a complete residual cylinder. Also the consolidation of several carpels into single compound fruit valves has a parallel in *Orobanche* (see under Orobanchaceæ later in the present Volume, Part 12, p. 457) and also in *Eschscholzia* (see under Papaveraceæ in Vol. I, Part 2, p. 52). The development in all *Gentiana* spp. of only two tracts of conducting tissue running up in the ovary wall is further evidence of this trend by synthesis towards the G 4 condition characteristic of the other genera in the Family.

**\*Chlora perfoliata.** Flower hypogynous. K 5-8 C 5-8 A 5-8 G 4, 2 sterile, 2 fertile. Median radial splitting of the fertile carpels which in other genera brings about dehiscence of the fruit takes place in the bud stage, the loculus thus communicating with the exterior by two opposite clefts which become closed later by conducting tissue. Stigmatic papillæ formed from this tissue fill the clefts but do not protrude through the openings to the exterior. Style terminated by two horseshoe-shaped stigmas standing in line with the sterile carpels. Fruit a capsule dehiscing through median radial splitting of the fertile carpels.

The sterile carpel midribs alone are prolonged into the style and extend to the stigma level, but each stigma plainly represents  $\frac{1}{2}$   $\times$   $\frac{1}{2}$  carpels, stigmatic papillæ being absent in the mid-line of each fertile carpel and continuous as a v-shaped crest over each sterile carpel and the half of the fertile carpel coherent with it on each side.

**\*Erythræa Centaurium** (Centaury). K 4 C 4 A 4 G 4, 2 sterile, 2 fertile. Stigmas 2, broad and entire.



## 140. APOCYNACEÆ

Flower ♂, actinomorphic, hypogynous or, exceptionally, slightly syngonous. Calyx, corolla, and androecium isomerous and generally pentamerous (K 5 C 5 A 5), rarely tetramerous (K 4 C 4 A 4). A disc generally present round the base of the ovary, either as a continuous ring with an entire or lobed margin or as 2-5 separate scale-like structures; only rarely in the absence of a separate disc structure is the wall of the ovary at its base glandular. Gynæceum generally pseudo-apocarpous through bifurcation of the axis with consequent median radial splitting of the fertile carpels, later through compression becoming syncarpous in the region of the style and stigma; seldom syncarpous throughout (*e.g.* *Allamanda*); still more rarely appearing to be apocarpous and to consist of additional ( $> 4$ ) carpels through median radial splitting of the sterile as well as the fertile members. Carpels 4, orthogonal, 2 sterile, 2 fertile, the median pair generally sterile and the lateral fertile; but when the disc is in the form of two median scales the lateral carpels are sterile and the median fertile. Ovary, when tetramerous and pseudo-apocarpous, incompletely bilocular at the base where the fertile carpels come into contact in the centre but do not fuse and have not yet become completely split in half; when syncarpous, bilocular or unilocular according as the fertile carpels extend to the centre or not. Styles in the tetramerous pseudo-apocarpous gynæceum 2, standing over the sterile carpels, distinct at first, becoming connate in the course of development; in the syncarpous gynæceum connate throughout. Stigma head, terminal, large, varying in form. Ovules generally numerous, rarely very few or only two. Fruit in syncarpous types simple, berry-like, drupaceous or capsuloid (*e.g.* *Allamanda*); in pseudo-apocarpous types of (almost

always) two partial folliculoid fruits, each of  $\frac{1}{2}$   $\times$   $\frac{1}{2}$  carpels, splitting down the mid-line of the fertile carpels.

### ILLUSTRATIVE TYPES

\***Vinca** (Periwinkle) (Fig. 28). K 5 C 5 A 5 G 4, 2 lateral, sterile, 2 median, fertile. Disc of 2 median vascular scales. Gynæceum pseudo-apocarpous, giving rise to two separate ovaries. Ovules few, borne in two rows on each fertile carpel. Styles 2, becoming connate in the course of development, enlarged at the top where the now single style is ringed by the stigma and then, projecting beyond this level, ends in two short hair-covered processes. Fruit of 2 follicles, each of  $\frac{1}{2}$   $\times$   $\frac{1}{2}$  carpels.

Sepals with commissural marginal veins. The vascular bundles for the stamens originate independently, leaving behind in the centre a complete vascular cylinder. Elements in this residual cylinder lying in the lateral plane to right and left are organised into the two sterile carpel midrib bundles. Of the elements forming the two (anterior and posterior) arcs some turn inwards and become organised into the twin placental bundles of two median fertile carpels; others turn outwards and enter the two median disc scales. This latter process leaves the remaining elements of each arc separated into two portions. At this stage the apex of the axis divides dichotomously a split appearing in the central parenchyma in the median plane. This split extends to the gynæceal tissue so that the gynæceum now consists of two lateral halves, consequently the two portions of each vascular arc which might otherwise be organised into a single fertile carpel midrib remain separate. Each half of the gynæceum thus forms a separate ovary composed of one sterile carpel flanked on each side by half a fertile carpel with the corresponding vascular systems. Immediately after the appearance

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FIG. 28. *Vinca major* (Periwinkle). Transverse sections through the flower base. A, from a level immediately above that at which the two lateral chambers of the ovary come into being. The vascular elements in the median plane are differentiated into two outer arcs which serve the anterior and posterior disc structures and into the placental strands of the two fertile carpels which have separated along their inner face but remain in contact. B, from a higher level after the ovary has become free from the surrounding perianth-andræcium ring. The fertile carpels have undergone median radial splitting, thus rendering the ovary pseudo-apocarpous. a stamen bundle, d disc bundles, f c b fertile carpel bundles, pl b placental bundles, p m petal midrib bundle, s c l sepal commissural lateral bundle not yet divided in two, s c m sterile carpel midrib bundle, s m sepal midrib bundle.

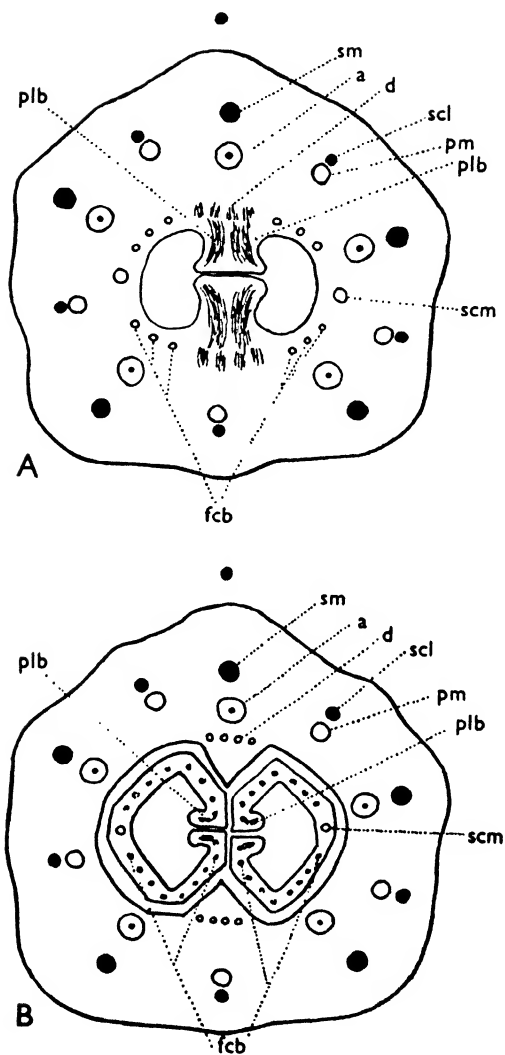


FIGURE 28.

of the loculus each ovary becomes split in the mid-line between the two half carpels thus bringing the loculus into communication at this level with the exterior, as commonly in ovaries of 1, or of  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels. As the two loculi close below the two styles the fertile carpel vascular systems coalesce with the sterile carpel midribs. The resulting compound bundles continue upwards, the (at this higher level) single style being traversed by two separate bundles throughout its length up to the stigma level where they break up into their components.

**Nerium Oleander** (Oleander). Disc o. Sterile carpels median, fertile carpels lateral. Ovules  $\infty$ , in numerous rows on each placenta. Flower otherwise as in *Vinca* (see above).

**Allamanda**. Disc ring-shaped. Gynæceum syncarpous, the sterile carpels median, the fertile lateral. Ovary unilocular. Ovules  $\infty$ , in numerous rows on each placenta. Flower otherwise as in *Vinca* (see above).

## 141. ASCLEPIADACEÆ

Flower always ♂, hypogynous or rarely slightly syngonous, with isomerous pentamerous outer whorls (K 5 C 5 A 5) and an oligomerous gynæceum of 2 median sterile and 2 lateral fertile carpels, pseudo-apocarpous as in Apocynaceæ (see under that Family earlier in the present Volume, Part 12, p. 433) owing to lateral dichotomy of the axis after the organisation of the vascular bundles for the perianth and andrœcium, with consequent formation of two separate ovaries, each consisting of  $\frac{1}{2} \times 1 \frac{1}{2}$  carpels and becoming cleft as in Apocynaceæ (see under that Family, *loc. cit.*). Ovules  $\infty$ , in numerous rows on each placenta. Styles 2, standing over the sterile carpels, united above in a single enlarged stigma head with which the andrœcium becomes fused, the whole structure (gynostegium) varying greatly in form, the terminal portion being sometimes flat and five-angled through pressure, sometimes conical, sometimes two-pronged. Stigmatic surfaces restricted to five positions corresponding with the intervals between the five stamens. [The occurrence of five separate receptive areas confined to one set of radii is not, as might at first appear, indicative of the presence of a corresponding whorl of five carpels, but follows necessarily from the fusion of the tissue of the stigma head with that of the stamens on the alternate set of radii, which prevents the formation of a continuous receptive ring such as occurs in Apocynaceæ, where the stigma head is free on its whole circumference.] Disc absent. Fruit of 2 folliculoid partial fruits.

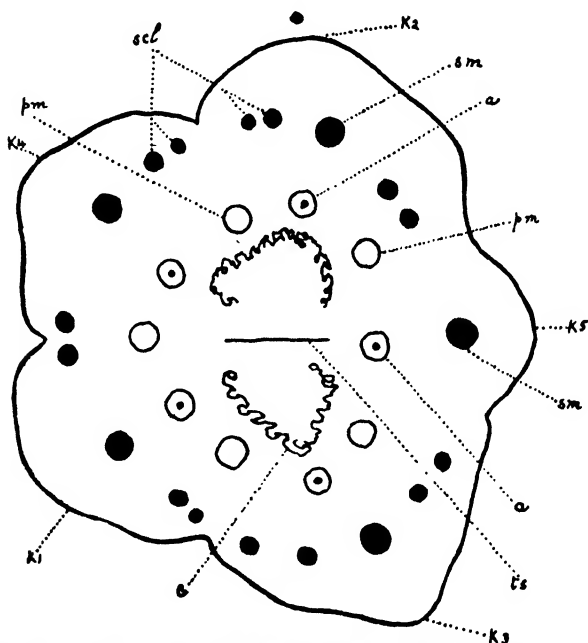
The vascular ground-plan is precisely similar to that of those types in Apocynaceæ in which the median carpels are sterile and the lateral fertile, and in which the disc is absent.

## ILLUSTRATIVE TYPES

**Asclepias, Ceropegia** (Fig. 29), **Hoya** (Wax flower). Apex of the stigma head flat and five-angled or only shortly conical.

**Stephanotis.** Apex of the stigma head tapering into a large cone.

**Araujia.** Stigma head surmounted by two prongs.



*Ceropegia dichotoma.* Transverse section through the flower base at the level at which the vascular tissue serving the gynæceum has divided into two median arcs preparatory to the bifurcation of the stem apex (indicated by the horizontal line *ts*). This premature division brings about the halving of the elements proper to each fertile carpel (here lateral) so that each resulting arc consists of the elements belonging to one sterile carpel flanked on each side by those belonging to half of one of the two fertile carpels.

*a* stamen bundle, *G* the arcs of (as yet) undifferentiated vascular elements belonging to a sterile carpel and half the fertile carpel on each side, *K* 1-5 the sepals in the order of their development, *pm* petal midrib bundle, *scl* sepal commissural lateral veins (those in the adjacent halves of sepals 1 and 3 and of sepals 2 and 4 have branched), *sm* sepal midrib bundle, *ts* line of division in the stem apex.

FIGURE 29.

## 142. CONVOLVULACEÆ

Flower ♂, actinomorphic, hypogynous, pentamerous in the outer whorls but rarely with an isomerous, generally with a dimerous gynæceum, K 5 C 5 A 5 G 2, median, sterile + 2, lateral, fertile, rarely 5 sterile + 5 fertile. Ovary almost always syncarpous and bilocular through fusion of the fertile carpels in the centre, with a single, forked terminal style; rarely pseudo-apocarpous with 'gynobasic' styles (*Dichondreæ*) owing to the unequal development of the sterile and fertile carpels. In the above-mentioned small section the fertile pair of carpels come to an end with the production of two or four basal ovules, hence the two sterile carpels, which form the wall of the two ovaries and the styles, become separate. As the ovules enlarge upwards they cause the middle region of these carpels to become curved over inwards and downwards so that eventually the styles appear 'gynobasic.' Stigmas as many as the styles or style branches, standing over the sterile carpels, varying in form. A ring-shaped disc surrounding the ovary base usually present. Ovules generally two in each loculus. Fruit berry-like and indehiscent or a capsule dehiscing at the apex.

## ILLUSTRATIVE TYPES

\**Convolvulus arvensis* (Bindweed). K 5 C 5 A 5 G 2, median, sterile + 2, lateral, fertile. Ovary bilocular. Style single, terminal. Stigma lobes 2, elongated. A five-sided ring-shaped disc surrounds the ovary. Fruit a four-seeded capsule.

Sepals with commissural marginal veins. The development of the stamen and carpel bundles proceeds centripetally instead of centrifugally as is the more usual method. This reversal of direction does not affect the alternation of these whorls, the sterile carpels and loculi in those genera which include fully isomerous forms being developed on the petal radii and the fertile carpels on the sepal radii. Only the sterile carpel midrib bundles are prolonged into the style.

## 143. POLEMONIACEÆ

Flower ♂, actinomorphic or sometimes slightly zygomorphic, hypogynous, pentamerous in the outer whorls (K 5 C 5 A 5), usually with an oligomerous (tri- or dimerous), rarely an isomerous gynæceum. Ovary syncarpous, with as many loculi as fertile carpels through the fusion of these carpels in the centre. Ovules 1-∞ in each loculus, when numerous 2-seriate. Style single, dividing above into as many stigmatic arms as there are sterile carpels, the arms standing over these carpels. An intra-staminal disc usually present. Fruit a capsule, generally with loculicidal combined with septifragal dehiscence through median radial splitting of the sterile carpels combined with the tearing of the fertile carpels (septa) so as to leave a central column with the attached seeds; rarely dehiscing septicidally through median radial splitting of the fertile carpels (*Cobæa*).

## ILLUSTRATIVE TYPES

**Phlox.** K 5 C 5 A 5 G (generally) 3, sterile + 3, fertile. Ovary sometimes becoming unilocular at the summit as the fertile carpels no longer extend to the centre. Stigmatic arms filamentous, papillose throughout their length. Ovules generally 1 or 2, rarely 3-5 in each loculus. Fruit a capsule with loculicidal combined with septifragal dehiscence.

Sepals with commissural marginal veins. The stamen vascular bundles originate independently. Midrib bundles present in the fertile as well as the sterile carpels, but only those of the sterile carpels prolonged up the style, one of these bundles entering each stigmatic arm.



## 144. HYDROPHYLLACEÆ

Flower ♂, actinomorphic, hypogynous, pentamerous in the outer whorls (K 5 C 5 A 5). Sepals generally with single or paired appendages. Corolla sometimes with paired or single scale-like outgrowths at the points at which the epipetalous stamens spring from the inner face (*Phacelia*). Disc seldom well developed. Gynæceum of 2 median, sterile and 2 lateral, fertile carpels. Ovary syncarpous, bilocular through fusion of the fertile carpels in the centre, sometimes becoming unilocular at the summit as these carpels become free on their inner face, or unilocular throughout when they at no level reach the centre and fuse. Ovules 2-∞ on each placenta, when numerous in several rows. Styles 2, distinct or connate below and separating above, standing over the sterile carpels. Stigmas terminal, punctiform or capitate. Fruit a capsule, dehiscing loculicidally through median radial splitting of the sterile carpels sometimes accompanied by the tearing of the fertile carpels (septa) so as to leave a central column with the attached seeds.

Vascular ground-plan similar to that of *Phlox* (see under Polemoniaceæ earlier in the present Volume, Part 12, p. 440).

## ILLUSTRATIVE TYPES

**Nemophila.** Sepals generally with appendages, single (*e.g.* *N. insignis*) or paired (*e.g.* *N. phacelloides*).

These appendages are supplied by the commissural marginal veins, each sepal segment receiving only the corresponding midrib bundle which forms true lateral branches. If the commissural vein arising on each petal radius from the trunk cord which also furnishes the petal midrib remains undivided it behaves like a midrib bundle giving rise to lateral veins. Only a single appendage is then formed between neighbouring sepals. But if each of these commissural veins forks sooner or later (as normally happens, since ordinarily these veins furnish a marginal system to the sepal on each side) then

either the single appendage becomes bifid or paired appendages alternate with the sepals ; one half of the single appendage or one appendage of the pair, as the case may be, properly belongs to the sepal on the one side and receives the corresponding branch of the fork, the other appendage or half appendage receiving the other branch. Hence in species with these appendages the sepal segments lack marginal veins. Similar paired appendages are formed in several *Lythraceæ*, though in this latter Family, owing to anastomosis, the vascular scheme is more complex (see under this Family earlier in the present Volume, Part 8, p. 274). Nevertheless, the presence in this latter Family of other genera without appendages and consequently with commissural marginal veins leaves no doubt that the appendages in the lythraceous genera are comparable with those in *Nemophila*, and are associated with the same vascular relations.

Ovary unilocular. Ovules 2-12 on each placenta. Styles 2, connate below, separating above. Stigmas terminal, capitate.

**Phacelia.** Sepals without appendages and with commissural marginal veins. Ovary uni- or bilocular. Ovules 2 on each placenta, collateral. Styles as in *Nemophila* (see above). Stigmas punctiform.

## 145. BORAGINACEÆ

Flower ♂, generally actinomorphic, rarely zygomorphic and then commonly with oblique symmetry (*e.g. Echium*), hypogynous, usually pentamerous with an oligomeric gynæceum (K 5 C 5 A 5 G 2, median, sterile + 2, lateral, fertile) rarely tetramerous throughout. Petals often with a hollow outgrowth varying in form at the top of the tube. Staminal filaments sometimes with a dorsal outgrowth (*Borago*), becoming free from the corolla at varying levels. Ovary surrounded by a ring-shaped disc into which some vascular elements enter but immediately come to an end; unilocular, but having the appearance of being quadrilocular. In the largest of the four sections into which the Family is divided (Boraginoideæ) both sterile and fertile carpels become partially split radially from without inwards, thus giving rise to a 4-lobed outline. Ovules 4, one in each lobe, two being borne by each fertile carpel. As the two sterile carpels become split the midrib bundles retreat towards the centre, remaining undivided; continuing upwards they enter the single style which is formed of these carpels only and which, owing to the upward swelling of the ovary lobes to accommodate the ovules, springs from between these lobes. Sooner or later the style forks through separation of the two component carpels, each arm (carpel) bearing an undivided stigma. Fruit of 4 one-seeded nutlets which separate through complete splitting of all four carpels.

That the level at which the style originates in the Boraginoideæ and the formation of four nutlets result from the above-described splitting of both kinds of carpels is shown by the fact that when, as is the case in the two small sections Cordioideæ and Ehretioideæ, this splitting is very slight, causing merely a furrow, the ovary remains

unlobed and the style is terminal. An intermediate condition occurs in a third section (*Heliotropoideæ*). For in some species of *Heliotropium* (*Heliotrope*) the fertile carpels undergo splitting but the sterile carpels remain undivided. Here the style is terminal but the fruit consists of two 2-seeded nutlets each composed of a whole sterile carpel flanked by half of the fertile carpel on each side.

## ILLUSTRATIVE TYPES

### BORAGINOIDEÆ

**\*Symphytum** (*Comfrey*). Flower actinomorphic. Petals with tongue-like, hollow outgrowths alternating with the anthers.

**\*Borago officinalis** (*Borage*) now naturalised in several counties. Flower actinomorphic. Petals with swellings at the throat. Staminal filaments with a dorsal appendage.

**\*Echium vulgare** (*Viper's Bugloss*). Flower zygomorphic with oblique symmetry, petals and stamens being of unequal size.

## 146. VERBENACEÆ

Flower ♂, generally more or less zygomorphic with oligomeric whorls in the gynæceum, sometimes also with suppression of some members in the andrœcium, rarely actinomorphic and isomeric (*e.g. Geunsia*). Calyx and corolla generally pentamerous or tetramerous. In flowers with a pentamerous perianth stamens rarely 5, all fertile or the posterior member staminodal (*e.g. Priva*), more often 4; in those with a tetramerous perianth stamens generally also 4. Gynæceum syncarpous, rarely isomeric with the andrœcium and having an even rounded outline as in *Geunsia* (K 5 C 5 A 5 G 5, sterile + 5, fertile), or as in *Duranta* (K 5 C 5 A 4 G 4, sterile + 4, fertile); carpels generally reduced to 2, median, sterile + 2, lateral, fertile. Ovary then four-lobed and unilocular but, as in most Boraginaceæ and in Labiatae (see under these Families in the present Volume, Part 12, pp. 443 and 447, respectively), appearing quadrilocular through the incomplete retraction of the midrib tissue of the sterile carpels into the ovary wall and the close approximation in the centre of the placentæ of the two fertile carpels.

In *Geunsia* and *Duranta* the ovaries, unilocular as in the dimerous gynæceum, become divided at some distance above the base by 10 and 8 complete partitions, respectively, and at these levels appear 10- and 8-chambered. These partitions arise through the complete fusion of the inner boundaries of the sterile carpels with the placental face of the neighbouring fertile carpel on each side while remaining separated from these same carpels laterally by the cavities occupied by the ovules.

Style single, generally terminal, sometimes more or less sunk between the lobes of the ovary ('gynobasic') formed by the sterile carpels which may remain connate to the end of the style and bear a bilobed stigma; or they

may separate into a corresponding number of arms with separate stigmas equally or unequally developed. Stigmas always in line with the sterile carpels and loculi. Fruit indehiscent, stone-like or breaking up into two or four stone-like portions through median radial splitting of the fertile, or of both sterile and fertile carpels.

Sepals with commissural marginal veins (*e.g.* *Duranta*), or without (*e.g.* *Verbena*). In types with C 5 A 4 the posterior stamen is usually suppressed without trace, morphological or vascular. Less often it persists as a minute process with a portion, or with the whole, of the corresponding vascular bundle. Or the process may still persist after the vascular bundle has been lost. Or a remnant of the bundle may survive after the process has wholly disappeared (see 22, p. 150, Figs. 33-36). Modification of the posterior stamen into a large sterile petaloid structure with pinnate venation occurs in *Stachytarpheta variabilis*. For other instances in which the normally unbranched vascular bundle of a stamen gives rise to a branched system when the corresponding member becomes sterile and the filament is modified from a radial into a dorsiventral structure, see Figs. 21 and 24; also 22, Figs. 1, 6, 7, 18, 19, 33 A, 33 B. And for the same development in a less marked degree, see later in the present Volume under *Salvia* (Labiatae), Part 12, p. 448, and 22, p. 146, Fig. 26). Style with as many vascular bundles as there are sterile carpels.

### ILLUSTRATIVE TYPES

**\*Verbena.** Flower slightly zygomorphic. K 5 C 5 A 4 G 2, median, sterile + 2, lateral, fertile. Ovary four-lobed, unilocular but appearing quadrilocular. Ovules 4. Style terminal. Stigma bilobed. Fruit splitting into four one-seeded stone-like partial fruits enclosed in the persistent calyx.

## 147. LABIATÆ

Flower ♂, zygomorphic, hypogynous. Calyx and corolla pentamerous, the calyx gamosepalous with five teeth or two-lipped, the corolla bilabiate. Andræcium generally tetramerous through suppression of the posterior member and didynamous (two long, two short); exceptionally, dimerous through loss, in addition, of the postero-lateral pair (*Rosmarinus*, most *Salvia spp.*, *Lycopus spp.*), very rarely of the antero-lateral pair (two *Salvia spp.*). Gynæceum always oligomerous. (K 5 C 5 A 4, seldom 2 G 4, 2 median sterile, 2 lateral fertile; 22, p. 148, Figs. 28-32.) Stamens springing from the corolla tube. Posterior stamen suppressed without trace of outward form or of the corresponding vascular bundle. Suppression of the two postero-lateral stamens may be similarly complete; or these members may take the form of minute staminodes with normally developed vascular bundles (*loc. cit.*, p. 142, Figs. 18-20, and p. 144, Figs. 22, 23); or the corresponding vascular bundles may persist when all morphological form has been lost (*loc. cit.*, p. 144, Fig. 21; for further details see below). Ovary surrounded at the base by a disc, unilocular, but as in the section Boraginoideæ of the Boraginaceæ (see under that Family earlier in the present Volume, Part 12, p. 443) appearing quadrilocular through protrusion into the loculus of the midrib tissue of the two sterile carpels and the close approximation of the large placentæ of the two fertile carpels. The gynæceum also resembles that of the Boraginoideæ in the single, more or less 'gynobasic' style formed of the two conjoined sterile carpels which separate above, each bearing usually an undivided stigma; in the four-lobed form of the ovary owing to the median radial splitting from without inwards of both pairs of carpels; in the number (four) and disposition (two on each

placenta) of the ovules; and in the form of the fruit (four nutlets).

Sepals with commissural marginal veins. If these veins are strongly developed the calyx tube is 10-ribbed or 15-ribbed according as the original commissural vein remains single up to the level at which the sepal segments separate, or as it gives rise in its course up the calyx tube to a marginal vein for the sepal on either side.

In those corollas, which show the fullest development of the vascular system, the midribs of all the petals give rise to a pair of primary laterals, generally at the base of the corolla-stamen tube (22, p. 140, Figs. 13, 17), sometimes near the top (*loc. cit.*, Fig. 14), sometimes at different levels (*loc. cit.*, p. 142, Fig. 19). Frequently in flowers of the two-stamened types the lateral vein on the side away from the median plane in each of the two postero-lateral petals is wanting, the one on the opposite side being still present (p. 142, Fig. 18 and p. 144, Fig. 21). This asymmetry gives further evidence of the decline in vigour in the two corresponding sectors, which has already led to complete loss of morphological form in the two stamens situated in these sectors, although the corresponding vascular bundles persist.

The stamen bundles originate independently and run upwards in the corolla tube. When, as in *Rosmarinus officinalis* and *Salvia schiedeana*, those for the postero-lateral pair persist, although these members are reduced to minute staminodes or do not attain even this degree of morphological form, these bundles fork at the staminode level, the two laterals thus formed giving rise to a marginal system in the petal on either side (*loc. cit.*, p. 142, Figs. 18, 19). A similar vascular development characterises the Primulaceæ and Theophrastaceæ in which the antesepalous stamen bundles persist, although the corresponding stamens are wanting, or, in the one or two genera in which they attain morphological form, are sterile (see under these Families earlier in the present Volume, Part II, pp. 409 and 402, respectively). A lesser development of the foliar type of venation accompanying sterilisation is also seen in the antero-lateral pair of stamens in *Salvia*. The connective in these stamens is forked, the one arm bearing a fertile half anther, the other ending in a sterile plate. The vascular bundle of the filament, in accord with this conformation, divides in two, the strand serving the half anther remains unbranched, the one supplying the sterile plate forms a branch system (*loc. cit.*, p. 146, Fig. 26).

Sterile carpels with, fertile carpels without, midrib bundles.



## ILLUSTRATIVE TYPES

**\*Lamium album** (White Dead Nettle) (22, p. 148, Figs. 28, 29). Calyx with five nearly equal teeth. A 4.

**\*Salvia spp.** (e.g. **\*S. Verbenaca**, Wild Sage, **S. officinalis**, Garden Sage) (22, *loc. cit.*, and p. 148, Figs. 31, 32). Calyx two-lipped, A 2.

## 148. NOLANACEÆ

Flower ♂, actinomorphic, hypogynous, pentamerous throughout. K 5 C 5 A 5 G 5, sterile + 5, fertile or G 5-25 (or more), sterile + 5-25 (or more), fertile. Gynæceum more or less pseudo-apocarpous through median radial splitting from without inwards of the fertile carpels. Ovary single, with as many loculi as sterile carpels, or with twice as many, each loculus being then sometimes sub-divided into as many secondary chambers as there are ovules through exceptional development of the parenchymatous tissue of the sterile carpels around the ovules. Or ovaries numerous, partially separate, developing successively as in Malopeæ (see under Malvaceæ in Vol. I, Part 4, pp. 108, 110), unilocular, rarely, 2-chambered. Ovules solitary or several in each loculus. Style single, 'gynobasic.' Stigma terminal, entire or lappeted. A ring-shaped disc present round the base of the gynæceum. Fruit of 5-10 partial fruits in one series, or of 10-30 in an irregular heap (sorema), arising through completion of the radial (septicidal) splitting initiated at an earlier stage, and further tearing of the carpel tissues in such a way as to leave behind on the axis the placentæ and the style. Partial fruits, each of  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels, 1-8-seeded, indehiscent.

## ILLUSTRATIVE TYPES

**Nolana** (30, pp. 423-431, Figs. 1-7, and 32, pp. 388, 389).

**N. prostrata** (*loc. cit.*, Figs. 1-5). Ovary single. Style cylindrical. Stigma entire. Partial fruits 5, 4-8-seeded.

**N. atriplicifolia** (*loc. cit.*, Figs. 6, 7). Ovaries  $\pm$  25. Style angled. Stigma lappeted. Partial fruits numerous 1- or rarely 2-seeded.

In both the above species the sepals have true lateral veins. Only the sterile carpel midribs are prolonged into the style filament, five bundles traversing the length of the filament in *prostrata*, 25-30 (or fewer) that of *atriplicifolia*. In the latter species the whole number are arranged in a pentagon corresponding with the 5-sided, 5-angled outline of the filament.

Limitation of ground-space in *atriplicifolia* causes the successively developed and partially separate 25-30 ovaries to become piled upon one another in a mound-like heap (sorema), development taking place uninterruptedly as in Malopeæ (*loc. cit.*), where spatial restriction leads to the formation of regular 'fields' of ovaries.

Successive development of the carpels where the number is very large occurs also in Punicaceæ, but in this latter Family development is not continuous as in *Nolana atriplicifolia* and in Malopeæ, but is rhythmic, taking place at 2 or 3 levels, with the result that the cyclic arrangement is retained, the spatial conditions being met by the formation of 1 or 2 inner rings which become over-arched by the earlier outer one (see under Punicaceæ earlier in the present Volume, Part 8, p. 277).

## 149. SOLANACEÆ

Flower ♂, hypogynous, generally actinomorphic and pentamerous in the outer whorls (K 5 C 5 A 5) with an oligomerous, obliquely directed gynæceum of 4 carpels, 2 sterile, 2 fertile; sometimes with a zygomorphic corolla (e.g. *Nicotiana* (Tobacco) with slight, *Salpiglossis* and *Schizanthus* with marked, zygomorphism); or with suppression in the andrœcium (e.g. *Salpiglossis* with A 4, *Schizanthus* with A 2); rarely with an isomerous gynæceum of 5 sterile and 5 fertile carpels (*Nicandra*). Gynæceum syncarpous. A disc usually present round the base of the ovary. Ovary with as many loculi as fertile carpels through union of these carpels in the centre; appearing sometimes to have twice this number at the base through the protrusion of the sterile carpels so far into the ovarian cavity at this level as to unite with the placental tissue of the fertile carpels, thus producing a quadrilocular condition (e.g. *Datura*, Thorn-apple). Ovules in numerous rows on each placenta. Style single. Stigma lobes, when distinct, as many as the sterile carpels and standing in line with these carpels. Fruit a berry or a capsule; when a capsule dehiscing sometimes septicidally (e.g. *Nicotiana*), sometimes loculicidally and septifragally (e.g. *Datura*) sometimes transversely by a lid (e.g. *Hyoscyamus*, Henbane).

Calyx quincuncial, the plane of symmetry of the dimerous gynæceum usually passing through sepal 1, less often through sepal 3, in contrast with the almost invariable ground-plan elsewhere in which the plane of symmetry coincides with an orthogonal plane and passes through sepal 2. (For the order of development of the sepals in the quincuncial calyx, see p. 149, Fig. 7.) In those types with an oligomerous andrœcium the one or three stamens suppressed are those which leave the plane of symmetry unchanged.

Sepals with true lateral veins. The vascular bundles for the stamens arise from the central cylinder independently.

Sterile carpels with, fertile carpels without, distinct midrib bundles. Only the sterile carpel midribs traverse the length of the style to the stigma level. If the placental bundles of the fertile carpels enter the base of the style they shortly come to an end.

### ILLUSTRATIVE TYPES

**\*Solanum** (*e.g.* **\*S. dulcamara**, Woody Nightshade, Bittersweet, **\*S. nigrum**, Black Solanum, **S. tuberosum**, Potato). K 5 C 5 A 5 G 2, sterile + 2, fertile. Corolla actinomorphic. Fruit a berry.

## 150. SCROPHULARIACEÆ

Flower ♂, hypogynous, generally with pentamerous perianth whorls (K 5 C 5), a zygomorphic corolla and an oligomerous andrœcium (A 4 through loss of the posterior stamen, didynamous (2 long, 2 short) or with A 2, postero-lateral); rarely with suppression of the posterior sepal, or with an actinomorphic corolla and an isomerous andrœcium (*Verbascum*, Mullein); always with an oligomerous gynœceum of 2 median, sterile and 2, lateral, fertile carpels. Disc ring-shaped or unilateral. Gynœceum syncarpous. Ovary bilocular. Ovules few or numerous in two or several rows. Style single. Stigma capitate or bilobed with the lobes in line with the sterile carpels. Fruit a capsule, dehiscing loculicidally, septicidally, or by pores; or very rarely a berry.

## ILLUSTRATIVE TYPES

**\*Verbascum** (Mullein). K 5 C 5, actinomorphic A 5 G 2 + 2. Fruit a capsule dehiscing septicidally through splitting in the mid-line of the fertile carpels.

**\*Digitalis purpurea** (Foxglove). K 5 C 5, zygomorphic with an open corolla tube. A 4 G 2 + 2. Fruit as in *Verbascum* (see above).

**\*Antirrhinum** (Snapdragon). K 5 C 5, zygomorphic with a closed corolla tube. A 4 G 2 + 2. Fruit a capsule dehiscing by pores.

**\*Veronica** (Speedwell) (19b, p. 214†, and 20, pp. 453-493†). An unstable genus showing all stages of transition from K 5 C 5 to K 4 C 4. Corolla zygomorphic with an open tube, long, or short with a rotate limb. A 2, postero-lateral G 2 + 2. Fruit a capsule dehiscing loculicidally through splitting in the mid-line of the sterile carpels.

**V. satureloides.** Some flowers K 5 C 5.

**V. Teucrium.** K 5 C 4, the posterior corolla segment with two vascular systems indicating its formation from the fusion of the two postero-lateral petals (20, p. 472, Figs. 52*a, b*).

**\*V. Chamædrys, V. pectinata.** Most flowers K 4 C 4, the posterior corolla segment as in *V. Teucrium* (see above) (20, p. 460, Figs. 19*a-c*; 19*b*, p. 214, Fig. 15).

**\*V. arvensis, \*V. Buxbaumii.** K 4 C 4, the posterior corolla segment sometimes with two vascular systems, sometimes with one (20, p. 458, Figs. 14*a, b*, and p. 456, Fig. 8).

**\*V. hederæfolia, \*V. Anagallis, \*V. spicata.** K 4 C 4, the posterior corolla segment with a single vascular system indicating 'condensation' following upon previous fusion of the two postero-lateral petals (20, p. 454, Fig. 4, and p. 476, Figs. 61*a-c*; p. 456, Fig. 12, and p. 468, Figs. 44*a-c*; p. 469, Figs. 46*a, b*).

In exceptional flowers in which one of the two stamens is missing the corresponding vascular bundle may persist, running its course in the corolla tube (see 22, p. 156, Fig. 44). In other exceptional flowers one or both stamens may become sterile and petaloid. These members then become incorporated into the corolla and are indistinguishable from the true petal segments (*loc. cit.*, Figs. 47 and 50). Thus, a feature which is normal and characteristic of *Soldanella* (Primulaceæ) and of *Jacquinia armillaris* (Theophrastaceæ) (see under these Families earlier in the present Volume, Part II, pp. 408 and 402, respectively) may appear as an abnormality in *Veronica*.

## 151. LENTIBULARIACEÆ

Flower ♂, zygomorphic, hypogynous. K 5, with 2-5 teeth forming two lips C 5, bilabiate, the anterior petal spurred. A 2 antero-lateral, the posterior and two postero-lateral members of the whorl being suppressed, G 4, orthogonal, sterile, forming the wall of the ovary + 2 (or ? more) fertile, forming a central column bearing  $\infty$  or rarely only two ovules. Ovary unilocular. Style single or wanting. Stigma lobes 2, centred over the median sterile carpels, the posterior smaller, or sometimes wanting. Fruit a capsule, generally dehiscent into two, sometimes into four valves along the line of alternate or of all sterile carpel midribs; less often opening by an irregular transverse tear or indehiscent.

## ILLUSTRATIVE TYPES

**\*Pinguicula** (Butterwort). Calyx with five or four distinct lobes forming two lips. Corolla open, with well-developed spur. Posterior stigma suppressed. Capsule splitting into two or four valves.

**\*Utricularia** (Bladderwort). Calyx with the 5 sepals conjoined in two entire or toothed lips, the posterior lip with 3, the anterior with 2 vascular bundles. Corolla closed. Spur short. Posterior stigma present but not functional. Capsule splitting into two valves, or opening by a lid through irregular tearing, or indehiscent.



## 152. OROBANCHACEÆ

Saprophytes. Flower ♂, zygomorphic, hypogynous. K 5 or 4 through suppression of the posterior sepal C 5, bilabiate A 4 through suppression of the posterior stamen G 2, 3, 4 or 6, sterile + 2, 3, 4 or 6, fertile. A disc often present around the base of the ovary, sometimes annular, sometimes anterior only and 3-lobed. Ovary unilocular throughout or becoming so almost at once as the fertile carpels withdraw from the centre. Style single. Stigma of very various forms, often bilobed, or discoid and more or less concave, or funnel-shaped, or peltate; less often tri- or quadrilobed or four-angled or capitate. Lobes when separate generally (? always) 'commissural'; sometimes through fusion compound and then presenting the illusory appearance of not being 'commissural' (see below). Ovules in several rows on each fertile carpel. Placentæ simple or forked. Fruit a capsule dehiscing in line with all, or with alternate, sterile carpels (see below).

An unusual feature of the ovary in some types having a basic ground-plan of 4 orthogonal sterile and 4 diagonal fertile carpels, is the approximation in pairs, in consequence of the degeneration (or loss) of the two lateral sterile carpels, of the fertile carpels bordering each of these disappearing carpels. As a result of this approximation the two 'commissural' stigma lobes proper to the fertile carpels of each pair may coalesce so that the resulting compound lobe, though standing over two fertile carpels, is actually centred over the intervening disappearing sterile carpel. A further outcome of the degeneration of the lateral sterile carpels with loss of the corresponding vascular bundles is that dehiscence of the fruit can no longer be effected in line with these carpels. Consequently when the four fertile carpels are approximated in two pairs the fruit splits only in the median plane. Each of

the two resulting valves consists of  $\frac{1}{2}$  1 [1] 1  $\frac{1}{2}$  carpels with two separate longitudinal bands of ovules corresponding with the two whole fertile carpels. Whereas when the four fertile carpels are equidistant through equal development of the four sterile carpels (as *e.g.* in *Orobanche Hookeri*) the capsule splits in the lateral as well as in the median plane. Each of the four resulting valves consists of  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels and has a single median band of ovules. These stages in 'condensation' leading to reduction in the gynæceum of *Orobanche* afford a clue to similar processes which have occurred within the genus *Gentiana* (see under Gentianaceæ earlier in the present Volume, Part 12, p. 431).

In having a pentamerous perianth and andrœcium ground-plan with a tetramerous unilocular gynæceum *Orobanche Hookeri* is comparable with *Parnassia palustris* (see under Saxifragaceæ earlier in the present Volume, Part 5, p. 148).

### ILLUSTRATIVE TYPES

**\**Orobanche* spp., e.g. \**O. major***, commonly parasitic on *Ulex* (Gorse), *Genista* (Broom) and other shrubby Leguminosæ, **\**O. elatior*** on *Centaurea*, **\**O. Hederæ*** on Ivy (*Hedera*) (Broomrape). K 4 C 5 A 4 G 4 orthogonal, sterile, the two lateral in process of disappearing, + 4 diagonal, fertile, more or less approximated in two pairs. Disc absent. Capsule dehiscing by splits in the median plane into two valves, each with two longitudinal bands of ovules.

The sepals more or less distinct. In species in which they are united into a pair of lateral 1- or 2-toothed segments each segment with two midrib bundles. Although the posterior stamen no longer attains separate morphological form the corresponding vascular bundle often persists.

**\**Lathræa*** (Toothwort). K 4 C 5 A 4 G 2, median, sterile + 2, lateral, fertile. Ovary bilocular at the extreme base where the fertile carpels are fused in the

centre, becoming unilocular as these carpels separate from each other along their inner face. Between the corolla tube and the ovary an anterior three-lobed disc. Stigma concave-peltate. Fruit a capsule splitting in the line of the sterile carpels into two lateral valves each consisting of a fertile carpel flanked on each side by half a sterile carpel ( $\frac{1}{2}$  r  $\frac{1}{2}$ ).

Sepals equal with true lateral veins. Style with two vascular bundles, each bundle representing a sterile carpel midrib fused with half the vascular system of the fertile carpel on each side.

## 153. GESNERIACEÆ

Flower ♂, hypogynous or partially or completely syngonous. Perianth pentamerous. Corolla rarely almost actinomorphic with a short tube (*e.g.* *Ramondia*, *Petrocosmea*, *Saintpaulia*), the andrœcium then sometimes isomerous (*Ramondia*) or oligomerous (*e.g.* *Petrocosmea*, *Saintpaulia*); almost always distinctly zygomorphic with a long tube, the andrœcium then always oligomerous, either A 4 and didynamous or A 2, the missing members being often represented by staminodes. A disc generally present, ring-shaped or reduced to five glandular structures or unilateral. Gynœceum always oligomerous, syncarpous, of 2 median, sterile and 2 lateral, fertile carpels. Ovary unilocular, sometimes bi- or even quadrilocular at the base when the fertile carpels or both pairs of carpels extend at this level to the centre. Ovules in numerous rows on each placenta. Style single. Stigma capitate or bilobed, the lobes standing in line with the sterile carpels. Fruit generally a capsule dehiscing into two or four valves through median radial splitting of only the sterile, or of both sets of carpels, rarely berry-like (*Columnea*).

Final stages in reduction from A 5 to A 4 and to A 2 are observable in *Petrocosmea* (A 4) and *Saintpaulia* (A 2). In these genera morphological form may persist in some degree after the disappearance of the corresponding vascular bundle; or the vascular bundle may still be present after distinct morphological form is no longer attained (see 22, p. 152, Figs. 37-42), the bundle running its course up the corolla tube and then either coming to an end as the petal segments separate or forking and giving rise to a marginal venation system in the neighbouring petal on each side, as regularly in similar circumstances in other Families, *e.g.* Myrsinaceæ, Theophrastaceæ, Primulaceæ, Sapotaceæ, and often in Labiataë, and as an abnormality, *e.g.* in Scrophulariaceæ (see under these Families earlier in the present Volume, Part 11, pp. 405, 402, 409, and 416, and Part 12, pp. 448 and 455, respectively).

## ILLUSTRATIVE TYPES

**Streptocarpus.** Flower hypogynous. A 2, antero-lateral. Disc ring-shaped. Ovary almost bilocular, the fertile carpels, though free on their inner face, being almost in contact in the centre. Stigma bilobed.

**Sinningia speciosa** (popularly known as 'Gloxinia'). Flower partially syngonous, A 4. Disc in the form of five glandular structures.

## 154. BIGNONIACEÆ

Flower ♂, generally through the position, less often through the size of the floral members, zygomorphic, hypogynous, with pentamerous perianth and andrœcium (K 5 C 5 A 5), but the posterior staminal member, generally staminodal, rarely fertile (*e.g. Rhigozum*) or wholly absent, the other four being didynamous and all fertile except in *Catalpa* in which the postero-lateral pair as well as the posterior member are staminodal. Gynæceum oligomerous, syncarpous, of 2 median, sterile and 2 lateral, fertile carpels. Ovary sometimes bilocular through fusion of the fertile carpels in the centre, more often unilocular as the fertile carpels become withdrawn from the centre. Ovules generally  $\infty$ , in several rows on each placenta, sometimes few and 2-seriate (*e.g. Rhigozum*). A ring- or cup-shaped disc generally present. Style single. Stigmas 2, in line with the sterile carpels. Fruit generally a capsule, dehiscing septifragally so that the outer wall becomes free from the septa (Bignoniæ) or through median splitting of the sterile carpels (Tecomeæ); seldom fleshy and indehiscent.

## ILLUSTRATIVE TYPES

***Rhigozum obovatum*.** Posterior stamen fertile. Ovary bilocular. Ovules few, in two rows in each locus. Stigma lobes unequal, centred over the sterile carpels. Disc basin-shaped.

Sepals with commissural marginal veins. Stamen vascular bundles originating conjoined with the sepal midrib bundles, hence possibly the functional equality of the posterior member with the other four members since the development of the corresponding vascular bundle will not be affected by spatial stringency in the same way as when it originates later and independently. Disc with numerous vascular strands which remain undifferentiated. Sterile carpels with, fertile carpels without, separate midrib bundles. Only the sterile carpel midribs are prolonged up the style.

**Incarvillea.** The posterior stamen usually sterile, rarely fertile or absent, the other four being fertile and didynamous. Ovary bilocular. Ovules in four rows in each loculus. Stigma lobes equal. Disc basin-shaped. Fruit a capsule, dehiscing loculicidally, dorsally and ventrally or only ventrally, *i.e.* in the mid-line of both sterile carpels or only of the posterior one.

The stamen vascular bundles originate independently.

**Tecoma.** Ovules in numerous rows in each loculus. Disc ring- or cup-shaped. Flower otherwise as in *Incarvillea spp.* (see above).

**Catalpa.** Only the antero-lateral pair of stamens fertile. Ovules in numerous rows in each loculus. Disc scarcely developed. Flower otherwise as in *Incarvillea spp.* (see above).

**Eccremocarpus.** Ovary with a short stipe, unilocular. Ovules in numerous rows on each placenta. Flower otherwise as in *Incarvillea spp.* (see above).

## 155. GLOBULARIACEÆ

Flower ♀, hypogynous, zygomorphic, pentamerous, but with reduction in the andrœcium and gynœceum. K 5 C 5 A 4 G 2, median, sterile + 2, lateral, of which one is fertile, one infertile. Ovary unilocular. Ovule solitary, pendulous from one of the lateral carpels. Style single. Stigma terminal. Fruit one-seeded, dry, indehiscent.

Sepals with commissural marginal veins. Corolla bilabiate. The posterior stamen suppressed without trace, but the corresponding vascular bundle frequently present in the gamopetalous region of the corolla. The vascular bundles for the stamens turn out from the central cylinder independently. Ovary often surrounded by a glandular ring. Sterile carpels with midrib bundles. The one fertile carpel with a vascular bundle which comes to an end at the level of origin of the ovule. The corresponding bundle of the infertile carpel now lost.

## ILLUSTRATIVE TYPES

**Globularia vulgaris.** See the characters of the Family.

The vascular bundle of the missing stamen often well developed. Style hollow throughout. The vascular bundles of the sterile carpels prolonged up the length of the style. Stigma with two lobes standing over the sterile carpels; sometimes with two smaller lobes alternating with the larger ones and corresponding with the fertile and the potentially fertile carpels; sometimes with only one smaller lobe corresponding with the fertile carpel; sometimes without distinct small lobes.



## 156. ACANTHACEÆ

Flower ♂, slightly or markedly zygomorphic, hypogynous. K 5, two sepals being sometimes completely fused C 5 A generally 4 fertile, didynamous, sometimes only 2 fertile through modification or suppression of the postero-lateral pair as well as the posterior member, rarely all 5 fertile (*Penstemonacanthus*), G 2 median, sterile + 2 lateral fertile. Ovary syncarpous, bilocular through union of the fertile carpels in the centre, sometimes becoming unilocular above as these carpels become free on their inner face, rarely unilocular throughout owing to obliteration of one of the loculi. Ovules 2 or  $\infty$  in two series in each loculus, rarely solitary. Style single. Stigmas 2, terminal, varying in form, centred over the sterile carpels. A disc almost always present, usually ring- or cup-shaped. Fruit generally a capsule dehiscent loculicidally, through median radial splitting of the sterile carpels, rarely a drupe.

Sepals generally with commissural marginal veins. The vascular bundles for the stamens originate independently and may persist when separate morphological form is no longer attained. Undifferentiated vascular elements often present in the disc. Sterile carpels with, fertile carpels without, separate midrib bundles.

## ILLUSTRATIVE TYPES

**Thunbergia spp.** Calyx sometimes scarcely more than an undulate rim (*e.g.* *T. laurifolia*) or segmented into a ring of  $\pm 15$  teeth, the teeth corresponding with the main lateral veins as well as the midribs (*T. Gibsonii*). Flower almost actinomorphic. Corolla, with five nearly equal lobes. A 4, didynamous, the posterior member being suppressed but the corresponding vascular bundle

has persisted. Disc ring-shaped. Ovary bilocular, becoming unilocular above. Ovules 2 in each loculus. Stigmas 2, each half-funnel-shaped. Fruit a capsule.

Only the sterile carpel midrib bundles are prolonged up the style, the vascular system of the fertile carpels coming to an end as the loculi close. The forking of these bundles into two equal veins at the stigma level appears to indicate that the sterile carpels are of the consolidated type, since branching of the midrib in valve carpels is ordinarily pinnate.

**Acanthus mollis.** Flower zygomorphic. A 4. Stigma lobes short.

**Fittonia.** Flower zygomorphic. A 2. Stigma lobes short.

**Peristrophe speciosa.** Flower zygomorphic. Corolla twisted so as to appear resupinate. A 2. Stigma lobes small.

## 157. MYOPORACEÆ

Flower ♀, hypogynous, with an actinomorphic or two-lipped corolla. K 5 C 5 A rarely 5 (*Myoporum sandwicense*), generally 4 through suppression of the posterior member and then didynamous G 2-5, sterile + 2-5, fertile. Gynæceum syncarpous. Ovary with 2-5 loculi in accord with the number of fertile carpels which extend to the centre, or with twice as many when the sterile carpels also form complete partitions. Style single. Stigma terminal; not enlarged, actinomorphic, or enlarged, oblique and zygomorphic. Ovules 1-8 in each loculus in the bilocular ovary, solitary in each loculus in ovaries with more than two loculi. Fruit a 2-10-celled, 2-10-sided drupe, rarely falling into one-seeded partial fruits.

The radial dimension of the sterile carpels varies, not only in different species, but even in the individual flower. Thus, an ovary constructed of two sterile and two fertile carpels may exceptionally become trilocular, the one sterile carpel not projecting into the loculus, the other extending to the centre and forming a complete partition. A similar doubling of the number of loculi when the sterile as well as the fertile carpels form complete partitions occurs in *Sesamum indicum* among Pedaliaceæ.

## ILLUSTRATIVE TYPES

**Myoporum.** K 5 C 5, actinomorphic A 4 (*M. sandwicense* excepted, see above), didynamous G 2-5 sterile + 2-5 fertile. Loculi 2-10. Stigma actinomorphic. Fruit a drupe.

Sepals with commissural marginal veins.

**Oftia africana.** K 5 C 5, slightly zygomorphic A 4, didynamous G 2, sterile + 2, fertile. Ovary bilocular, becoming unilocular above. Stigma enlarged, oblique, zygomorphic.

Sepals with true lateral veins.

## 158. PLANTAGINACEÆ

Flowers generally ♂, sometimes unisexual, actinomorphic, hypogynous. Perianth and andræcium almost always tetramerous (K 4 C 4 A 4). Gynæceum usually of one orthogonal tetramerous whorl (G 2, median, sterile and 2, lateral, both being fertile, or one of the two barren). Ovary bilocular, sometimes becoming unilocular above, or unilocular throughout when the fertile carpels do not extend to the centre. Style single. Stigmas 'commissural,' the terminal stigmatic papillæ extending down almost the entire length of the style in two lines corresponding with the opening of the stylar canal to the surface in the mid-line of the split fertile carpels, or in four lines if the edges of the two channels thus formed become reflexed. Ovules generally 2-∞, sometimes single and then borne at, or near, the base of the ovary. Fruit a membranous capsule dehiscing transversely, or one-seeded and indehiscent.

## ILLUSTRATIVE TYPES

**\*Plantago** (Plantain). K 4, diagonal C 4, orthogonal A 4, diagonal G 4, orthogonal (2 median sterile, 2 lateral fertile). Ovary bilocular, but sometimes presenting an illusory appearance of being tri- or quadrilocular (*P. major*, *P. Coronopus*) through one or both placental cushions becoming so enlarged as to come into contact with the ovary wall. Fruit a capsule dehiscing transversely (pyxidium).

The diagonal position of the four sepals—an arrangement of rare occurrence—indicates that the existing tetramerous ground-plan has been derived from a pentamerous one through (1) complete loss of the posterior sepal, (2) complete congenital union of the two posterolateral petals and consequent development of only one

midrib, and (3) complete disappearance of the posterior stamen together with its vascular bundle.

The appearance of this final stage of reduction with no existing evidence of intervening steps is paralleled in some species of *Veronica* (e.g. *Anagallis*, *aquatica*, *acinifolia*, *Cymbalaria*, *glauca*, *hybrida*, *spicata*, see earlier in the present Volume under Scrophulariaceæ, Part 12, p. 455; also 20, Table facing p. 472 and numerous Figures).

In its earliest stage of development the ovary presents an appearance similar to that of a typical crucifer as regards the size and form of the two pairs of carpels. But as only one whorl of stamens is present in *Plantago*, as compared with two in Cruciferae, the disposition of the two carpel pairs is reversed, the sterile pair in *Plantago* being median and the fertile lateral, while in Cruciferae the sterile are lateral and the fertile median.

Sepals with true lateral veins. The vascular bundles for the stamens originate independently, but in some species the basal region of the bundles connecting with the central cylinder is no longer differentiated. Sterile carpels with, fertile carpels without, a midrib bundle. The placental bundles of the fertile carpels 'condensed' into a solid central column.

**\*Littorella lacustris.** Flowers unisexual, monœcious. ♂ Flower. K 4, orthogonal, 2 outer lateral, 2 inner median C 4, diagonal, A 4, orthogonal. ♀ Flower. Perianth single. Tepals 3 or 4 A o G 4, 2 median sterile, 2 lateral, of which one is fertile and one barren. Ovary bilocular. Ovule single, borne near the base in the larger loculus. Fruit one-seeded, indehiscent.



## Part 13

### Dicotyledons

Family	159.	Rubiaceæ
„	160.	Caprifoliaceæ
„	161.	Adoxaceæ
„	162.	Valerianaceæ
„	163.	Dipsaceæ





## 159. RUBIACEÆ

Flower ♂, generally actinomorphic and completely syngonous, rarely zygomorphic or only partially syngonous; generally tetramerous, less often pentamerous with reduction in the gynæceum, still less often pentamerous with an isomerous gynæceum. (K 4, orthogonal C 4, diagonal A 4, orthogonal G 4, orthogonal, the 2 median sterile the 2 lateral fertile; or K 5 C 5 A 5 G 4, as above; or K 5 C 5 A 5 G 5, sterile + 5, fertile.)

Sepals sometimes reduced to small teeth or lacking. Corolla with a longer or shorter tube. Stamens springing from the corolla tube. Ovary usually bilocular but unilocular if the fertile carpels fail to reach the centre, rarely 3-5-locular. A ring-shaped disc or separate glands usually present round the base of the style. Style single below, dividing at, or at varying distances below, the stigma level into as many arms as there are sterile carpels, the arms standing over these carpels. Ovules 1-∞ in each loculus. Fruit capsuloid, dehiscent loculicidally, or septicidally, or falling into cocci; or baccate or drupaceous.

### ILLUSTRATIVE TYPES

#### GALIEÆ

Stipules foliaceous. Ovary bilocular. Ovules solitary in the loculi, borne midway in the septum.

The stipular appendages may vary in number from node to node, and are indistinguishable from the two opposite leaves to which they belong. The appearance is thus produced of whorls of leaves from 4-10 in number. The true leaves can be identified on inspection by the presence of axillary buds and in transverse section by the vascular arrangement.

At any node only two bundles turn radially outwards from the central cylinder. These bundles, which are formed on opposite sides of the 4-angled stem, give rise at once to a pair of lateral branches. The central portion of each of the original bundles becomes the midrib bundle of the corresponding leaf. The four lateral branches follow a tangential course until they meet midway between the two leaves. From this vascular girdle, one, two, three or four bundles run radially outwards on each side of the stem between the leaves and enter a corresponding number of stipular appendages. If the development on the two sides is equal the apparent whorl will consist of an even number of leaf-like structures, if unequal, of an odd number.

**\**Asperula odorata*** (Woodruff). K 4 C 4 A 4 G 4, 2 median sterile, 2 lateral fertile. Sepals small. Corolla tube long. Stamens springing from near the top of the tube. The two seeds adherent to the fruit wall.

**\**Galium aparine*** (Cleavers, Goosegrass). Ground-plan as in *Asperula* (see above). Sepals wanting. Corolla tube very short so that the stamens become independent almost at once. Seeds as in *Asperula* (see above).

**\**Sherardia arvensis*** (Field Madder). Flower with a persistent calyx of either four or six teeth, otherwise as in *Asperula* (see above).

At the flower base the vascular system consists of ten trunk cords, three which turn outwards in the anterior and in the posterior sectors and twin cords remaining near the centre in each lateral sector. A strand given off from one side of each of these two central cords supplies the two ovules. At the top of the ovary the ten cords converge and anastomose. After this process of reconstruction four bundles pass up into the corolla tube and become the petal midribs and two into the style, corresponding with the two sterile carpels which below this level are without an independent vascular supply. The staminal filaments are without a differentiated vascular bundle.

In *Asperula* the venation scheme of the corolla presents on inspection an illusory appearance of resembling that of the Compositæ and Goodeniaceæ in which two Families the petals are characterised by having marginal veins of commissural origin (see under these Families later in the present Volume, Part 14, pp. 516 and 509, respectively). In *Asperula*, as in other Rubiaceæ (including *Putoria*, cited with *Asperula*

by Robert Brown in this connection under the name *Ernodea*), the marginal veins of the petal segments are, in fact, true lateral veins. These lateral veins are given off from the petal midribs at the base of the long corolla tube and run a parallel course up the tube which thus is traversed by twelve veins. At, or about, the level at which the staminal filaments spring from the tube the adjacent laterals of neighbouring petals converge and 'kiss.' They then diverge from these midway points between the petal midribs and form the marginal veins of the separate petal segments. They thus give the appearance of being of commissural origin. But, when the tube is split open, their true origin is revealed. The convergence of these laterals to the points at which the staminal filaments become disjoined from the corolla is possibly associated with the non-vascular condition of the filaments which have lost their own vascular bundles. Should a petal midrib fail to develop one of the two primary laterals the adjacent lateral of the neighbouring petal on that side forks as the petal segments are about to separate and thus provides the marginal vein for both petals (unpublished).

In *Galium* the primary laterals of the petals diverge at once from the midribs, but not sufficiently far for those of neighbouring petals to 'kiss.' Instead, a short transverse strand connects them at the level of nearest approach.

In *Sherardia* the vascular scheme is modified at the summit of the ovary in accord with the formation of a vascular calyx of six or four segments. Of the six original trunk cords which turned outwards at the flower base all (or sometimes only four) continue their upward course and pass directly into the six (or four) sepals. But part way up the length of the sepals they reverse their course, and turning through an acute angle return below the exertion level and there anastomose as in *Asperula*, forming a complex from which the four petal midribs and two style bundles take their rise. Although the corolla tube is long, as in *Asperula*, the connection between the petal primary laterals is made, as in the short-tubed *Galium*, by a short transverse strand.

## 160. CAPRIFOLIACEÆ

Flower ♂, actinomorphic or zygomorphic, syngonous. K 5 C 5 A 5, rarely 4 and didynamous (*Linnæa*, *Dipelta*) G 2-5, sterile + 2-5, fertile, or rarely both carpel whorls 5-8-merous (*Leycesteria*). Ovary with as many loculi as fertile carpels through union of these carpels in the centre. Ovules 1-many in each loculus. Styles, when present, separate through median radial splitting of the fertile carpels, centred over the sterile carpels, very short, channelled; or connate and long. Stigmas when styles wanting or very short as many as the sterile carpels and centred over these carpels; when the style is single confluent and capitate. Fruit a berry or berry-like drupe.

Sepals generally (? always) without commissural marginal veins. Stamen vascular bundles conjoined at first with the sepal midrib bundles, becoming free as the perianth separates from the summit of the ovary. Carpels without separate midrib bundles in the region of the ovary where only the placental bundles of the fertile carpels are differentiated.

## ILLUSTRATIVE TYPES

**\*Sambucus** (Elder). Flowers in corymbose heads. Corolla actinomorphic. G (generally) 3, sterile + 3, fertile. Stigmas sessile or almost so. Fruit a berry-like drupe.

**\*Lonicera** (Honeysuckle). Flowers in stalked cymose clusters or paired through suppression of the terminal flower of a three-flowered cyme. Corolla zygomorphic. G (generally) 3, sterile + 3, fertile. Style single. Stigma capitate. Fruit a berry.

**\*L. Periclymenum** (Common Honeysuckle). Flowers in stalked clusters. Berries separate.

**\*L. Xylosteum** (Fly Honeysuckle). Flowers paired. Berries united at the base.

**L. cærulea.** Flowers paired. Berries completely united into a single fruit.

In species with paired flowers a single central vascular cylinder remains after the bundles for the accompanying bracts have turned outwards. As this cylinder breaks up into the ten cords supplying each flower, seven turn radially outwards to the free side of each flower, three complete each of the two new cylinders on the contact side of each flower, but the intervening ground tissue remains undivided for a longer or shorter distance. Thus although the vascular systems become completely separated the basal regions of the two flowers arise united together and remain so up to varying heights.

**Viburnum Tinus** (Laurustinus). Corolla actinomorphic. G (generally) 3, sterile + 3, fertile. Style short. Stigmas distinct, 3. Ovary trilocular becoming unilocular in the one-seeded fruit through obliteration of the two barren loculi.

**Symphoricarpus racemosus** (Snowberry). Corolla almost actinomorphic. G (generally) 4, sterile + 4, fertile. Style elongated. Stigma capitate. Ovary quadrilocular, showing an unusual feature in that two ovules are formed in each median loculus, but only one in each lateral loculus. Only the solitary ovules furnish seed.

## 161. ADOXACEÆ

Inflorescence generally a five-flowered globular head (glomerule). Immediately beneath each flower a varying number of bracts, generally 3 if the flower is pentamerous, 3 or 2 if tetramerous, 2 or 1 if trimerous (a rare exception), 3 or 4 if hexamerous (a not infrequent variation). When 2-4 conjoined at the base simulating a gamophyllous whorl. Flower ♂, five-whorled through absence of a second perianth whorl, actinomorphic, partially syn-gonous, isomerous throughout. The central terminal flower generally tetramerous. T 4, diagonal A 4, orthogonal, each split into two filaments bearing half anthers G 4, diagonal, sterile + 4, orthogonal, fertile. The four decussately-arranged axillary flowers generally pentamerous. T 5 A 5, split in two as in the terminal flower G 5, sterile + 5, fertile. Ovary with as many loculi as fertile carpels through the union of these carpels in the centre. Ovules solitary in each loculus, pendulous from the inner angle near the top. Above the ovule level the fertile carpels become withdrawn into the ovary wall. Styles connate below into a short widely open tube, free above, as many as the sterile carpels and centred over these carpels. Stigmas terminal. Fruit a berry.

The disposition of the four tepals of a tetramerous perianth in the diagonal planes is a rare arrangement. It occurs also in *Petiveria* (Phytolaccaceæ) though another genus in this Family, *Rivina*, with the same numerical ground-plan has the four tepals in the more usual position in the orthogonal planes (see under Phytolaccaceæ earlier in the present Volume, Part 10, p. 371).

A difference in the numerical ground-plan according as the flower is terminal or axillary is a characteristic feature in a few genera in other Families, notably in Rutaceæ. But in this latter Family this relation,

as is more usual, is reversed, the fuller (pentamerous) ground-plan occurring in the terminal flower, the reduced (tetramerous) ground-plan in the lateral flowers.

A midrib with laterals may be present in each bract or a differentiated system may be lacking in one or more. Above the bract level the vascular ground-plan shows considerable irregularity. Owing to 'condensation' the number of cords which turn outwards to provide the tepal and stamen bundles is always fewer than the number of these members. Sometimes the bundles of the tepals and stamens turn outwards independently, sometimes those of a neighbouring tepal and stamen arise conjoined, lateral disjunction taking place later. These variations occur even in the individual flower. Furthermore, the distance from the centre at which disjunction occurs and at which the independent staminal bundle bifurcates also varies. Hence a central cylinder can hardly be said to have an existence at these levels, but the fact that the pairs of staminal filaments alternating with the tepals bear half anthers shows that bifurcation always occurred before the determinate phase had been reached. [Elsewhere whole stamens are developed when halving of the vascular elements serving a staminal member takes place outside the residual vascular cylinder, the determinate phase having then been reached; and, on the other hand, filaments with half anthers (as in *Adoxa*) when halving of the delimited staminal vascular tissue takes place within the residual cylinder and accordingly before the determinate phase has been reached, as in *Papaveraceæ-Fumarioideæ* and in *Malvaceæ* (see under these Families in Vol. I, Part 2, p. 48, and Part 4, p. 106, respectively).] The sterile carpel midribs are prolonged into the style tube. The fertile carpels are without midrib bundles; placental strands are present, but do not become fully differentiated until later.

The tepals, being without marginal veins of commissural origin, are green (see Vol. I, Introduction, p. 10 and 19*b*, p. 205). For the reverse relation—that in which the tepals have marginal veins of commissural origin and are coloured (*i.e.* are non-green) wholly or in part—see references under *Rivina* (*Phytolaccaceæ*) earlier in the present Volume, Part 10, p. 371.

## ILLUSTRATIVE TYPES

**\**Adoxa Moschatellina*** (Moschatel). See the characters of the Family.

## 162. VALERIANACEÆ

Flower ♂, irregular through asymmetric reduction in the andrœcium and gynœceum ground-plan, syngonous. Calyx rarely of five distinct sepals, generally more or less rudimentary; sometimes in the form of a pappus of 10 or more rays, or of 2-4 or more teeth, or of an entire rim. Petals 5, the anterior member often with a pouch or spur. Andrœcium alternating with the corolla, always oligomerous through suppression. Stamens 4 (*Patrinia* except *P. monandra*), 3 (e.g. *Valeriana*, *Valerianella*), 2 (*Fedia*), or 1 (*Centranthus*). Gynœceum syncarpous. Carpels 3, sterile + 3, of which only one is fertile. Style single, stigmas generally as many as the potentially fertile carpels and superposed upon them ('commissural'). Ovary unilocular except in those types where in addition to the original large fertile loculus two very small barren ones make their appearance. Ovule single, pendulous. Fruit one-seeded and indehiscent.

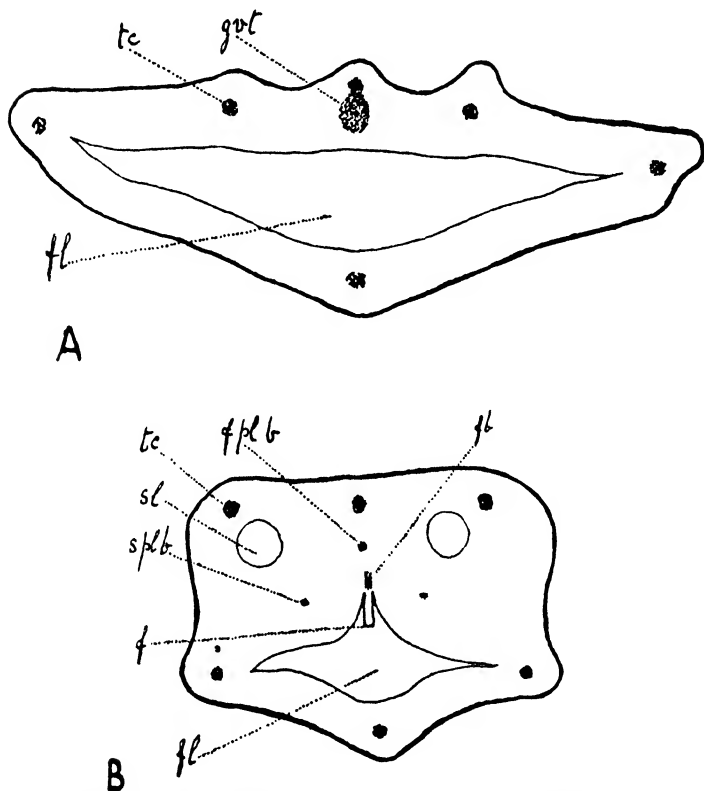
## ILLUSTRATIVE TYPES

**\*Valeriana** spp. (e.g. **\*V. officinalis** ♀, **\*V. dioica** unisexual and diœcious with sterile organs of the other sex in both ♂ and ♀ flowers). K in the form of a pappus of 10 or more rays C 5, tubular below with an anterior pouch, A 3 G 3 + 3. Stigmas 3, 'commissural.' Two small barren loculi present at the top of the ovary (see Fig. 30).

Owing to the sterility of two of the three inner carpels and the almost complete obliteration of two of the three loculi the gynœceum exhibits a highly exceptional construction. The three inner carpels arise completely fused with each other and with the wall of the ovary on the radius lying midway between the two barren loculi, only



assuming independent morphological form when these loculi make their appearance and the three placentæ become defined.



*Valeriana dioica* ♀. Transverse sections through the ovary. A, at the level at which the vascular tissue which gives rise to the placental bundles is becoming detached as a single strand from one of the six trunk cords arranged in a ring round the one fertile loculus which at a higher level anastomose forming a girdle from which the perianth-stamen bundles take their rise. B, at the higher level at which the above-mentioned single strand seen in A has divided into the three placental bundles of the three carpels. (The number of carpels is indicated by the three loculi of which two are sterile.) In the fertile loculus is seen the cut end of the funicle from which the rest of the ovule has been removed.

*f* funicle, *fplb* fertile carpel placental bundle, *fplb* fertile carpel placental bundle, *gvt* vascular tissue from which the placental bundles are formed, *sl* sterile loculus, *splb* sterile carpel placental bundle, *tc* trunk cord.

FIGURE 30.

Further evidence of this construction is furnished by the vascular system. This system consists at the flower base of six trunk cords which run up in the wall of the ovary. Three of these cords lie on the radii of the three loculi, and although no component is detached from these cords their position indicates that the midrib bundles of the three sterile carpels are (or if now lost were once) components of these cords. The three other cords lie on the alternate radii. Shortly above the level of origin of the fertile loculus a component is detached from the one of these cords which lies on the radius between the two barren loculi. This detached component consists of the conjoined bundles of the three potentially fertile carpels which are still fused with the ovary wall. Towards the summit of the ovary this compound component breaks up into three bundles, one bundle passing to each placenta and continuing up into the style. The one serving the fertile placenta gives rise to the strand of the funicle. This whole construction presents some points of resemblance with that of *Parinarium* among Rosaceæ, which similarly has a ground-plan of  $G\ 3 + 3$  in which only one loculus is developed and only one of the inner carpels fertile. But owing to the 'gynobasic' position of the style in *Parinarium* and the modifications which go therewith, the comparison cannot be carried further (see under Rosaceæ earlier in the present Volume, Part 5, p. 179; also 7, p. 612, Figs. 200-202, and pp. 614, 615).

As the exertion level is reached the six original trunk cords anastomose, forming a vascular girdle from which arise the several bundles for each ray of the pappus and for each petal and stamen.

**\*Valerianella spp.** (Corns salad). Calyx in the form of an entire or toothed rim. Otherwise as in *Valeriana* (see above).

**\*Centranthus ruber** (Red Valerian). Anterior petal spurred. A 1. Stigmas 3 or 2, 'commissural.' Barren loculi often completely obliterated. Otherwise as in *Valeriana* (see above).

## 163. DIPSACEÆ

Inflorescence a capitulum surrounded by an involucre of bracts, with or without other bracts subtending the florets. Florets surrounded at the base by a cup-shaped structure of connate bracts (involucel), syngonous, zygomorphic. Calyx and corolla pentamerous (*e.g.* *Scabiosa spp.*) or tetramerous (*e.g.* *Dipsacus*, *Knautia*), alternate (see below). Corolla gamopetalous. A 4, the posterior member in pentamerous types being suppressed. G derived from a ground-plan of 3, sterile + 3, fertile as in *Valeriana* (see under Valerianaceæ earlier in the present Volume, Part 13, p. 480), but showing still greater reduction (see below). Ovary unilocular. Ovule solitary, pendulous in the posterior mid-line from near the top of the loculus. Style 1, obliquely truncate. Stigma terminal, zygomorphic, being in the form of an oblique-rimmed but medianly symmetrical funnel. Fruit generally surrounded by the involucel and crowned with the persistent calyx, one-seeded, indehiscent.

The several isomerous whorls alternate in the tetramerous as in the pentamerous forms. In *Dipsacus pilosus*, a tetramerous type, the four angles of the four-sided calyx stand in line with the four midrib teeth of the bracts of the involucel to the exterior and with the four petals to the interior. The appearance that the angles of the calyx represent the mid-line, *i.e.* the midribs of the sepals, and that, in consequence, bracts, sepals and petals are to be regarded as superposed, is illusory. These angles correspond, in fact, to the projecting junctions, and the mid-line of the flat sides to the mid-line of the sepals. Hence bracts, sepals and petals regularly alternate.

The gynæceum resembles that of *Valeriana* in the following characters:—(1) The three outer sterile carpels

lack separate midrib bundles; (2) the three inner carpels together form a single column of tissue fused in the posterior mid-line with the wall of the loculus into which it protrudes; (3) this column has a central vascular core which towards the top of the ovary breaks up into three placental bundles, the strand to the ovule being derived from the middle and strongest of the three bundles. But it has undergone still further reduction, for the two barren loculi have become completely obliterated and are no longer traceable. The three placental bundles are generally prolonged up the style to the stigma level, the fertile bundle running to the highest point of the oblique rim, the barren ones to points on the lower side of the rim.

### ILLUSTRATIVE TYPES

**\*Dipsacus** (e.g. **\*D. pilosus**, Small Teasel, **\*D. sylvestris**, Common Teasel). Involucel of 4 connate bracts. K 4-angled, of 4 flat sepals C 4 A 4.

In the tetramerous *Dipsacus pilosus* the vascular system at the flower base appears in transverse section as an outer ring of eight trunk cords and an interrupted circle of residual elements in the centre. Four of the trunk cords furnish the sepal midribs and stamen bundles; the alternate four similarly furnish commissural marginal veins to the sepals and the petal bundles. The central residual elements become consolidated into a single strong cord which, as the loculus makes its appearance, runs up one side of the enclosing wall and takes up its position on the radius of one of the eight cords. Near the top of the loculus this cord breaks up into three placental bundles (see above in the account of the Family).

**\*Knautia arvensis**. Involucel as in *Dipsacus* (see above). K 4, ending in bristles in the mid-line and at the junctions C 4 A 4. The vascular scheme as in *Dipsacus* (see above).

**\*Scabiosa** (e.g. **\*S. Columbaria**). Involucel with an 8-ribbed frilled rim K 5 (bristles) C 5 A 4.

In *Scabiosa* spp., as in *Dipsacus*, the four-sided involucel and the andræcium are tetramerous, but the intervening whorls of the calyx and corolla, unlike those of *Dipsacus*, are pentamerous. Also, as in *Dipsacus*, the vascular supply for the

above-mentioned three floral whorls is derived from a ring of eight vascular cords lying on equidistant radii. Four of these cords give rise to the midrib bundles of four sepals and to the superposed stamen bundles. Three alternating cords become petal midribs. As the middle portion of the eighth cord turns outwards to become the midrib bundle of the fifth sepal the two lateral portions are left behind. These lateral portions of the original cord become the rather closely approximated midrib bundles of the two postero-lateral petals. No staminal bundle is formed between them, so that the vascular ground-plan now accords with the floral ground-plan 'K 5 C 5 A 4'. *Scabiosa* thus affords an example of a type in process of transition from a pentamerous to a tetramerous condition in the perianth-androecium whorls. From near the exertion level upwards the vascular and floral ground-plans of the perianth are typically pentamerous. Below this level the vascular ground-plan is tetramerous and similar to that of *Dipsacus*, in which the tetramerous condition has become fixed in all the outer whorls. To arrive at this latter condition from the *Scabiosa* type of construction all that is required is (1) that the posterior sepal should become suppressed, (2) that in consequence the two postero-lateral petals should become completely united, and (3) that the two corresponding midribs now arising from a common starting point should become a single bundle. The tetramerous condition would then become established as in *Dipsacus pilosus*. All these steps in the transition from pentamery to tetramery can be observed within a single genus in *Veronica* (see earlier in the present Volume for a fuller account, pp. 454 and 469), but in *Scabiosa* only one stage has been accomplished and this only in individual species. In *S. atropurpurea*, although the posterior sepal is still developed, the two postero-lateral petals have become united into a single structure in which, however, the two corresponding midribs still persist. The vascular scheme of the gynæceum as in *Dipsacus* (see above).

**Morina.** K 4 (the posterior sepal being suppressed), the antero-lateral and postero-lateral members on both sides united partially or completely, C 5 A 4 (two being staminodal), the posterior member being suppressed. The vascular scheme of the gynæceum as in *Dipsacus* (see above).

The initial step in the process of transition from a pentamerous to a tetramerous perianth in *Morina* occurs in the calyx instead of in the corolla as in *Scabiosa atropurpurea* (see above). Owing to the large size of the ovary the vascular scheme is particularly easily observed.



## Part 14

### Dicotyledons

Family	164.	Cucurbitaceæ
„	165.	Campanulaceæ
„	166.	Goodeniaceæ
„	167.	Stylidiaceæ (Candolleaceæ)
„	168.	Calyceraceæ
„	169.	Compositæ





## 164. CUCURBITACEÆ

Flowers (one genus, *Schizopepon*, excepted) unisexual, monœcious (e.g. *Cucumis*, *Cucurbita*, *Ecballium*, *Echinocystis*, *Luffa*) or diœcious (e.g. *Bryonia dioica*, *Fevillea*, *Thladiantha*), syngonous. The basic ground-plan, K 5 C 5 A 5 + 5 G 5, sterile + 5, fertile, is never completely realised in any existing form. The antesepalous staminal whorl is lacking in every genus except *Fevillea* in which it is present in the form of staminodes. In no species are more than three members of the antepetalous staminal whorl developed, though the duplication of two of the three members produces in all species reaching this level an illusory appearance (hitherto accepted as real) that the full five members are present. Divergence of the twin filaments so produced (when separate) and the consequent approximately equal spacing eventually of the resulting five stamens has led to the similarly deceptive (and hitherto also misinterpreted) appearance that the five stamens represent the antesepalous whorl (see 34). This erroneous interpretation necessarily involves acceptance of the anomalous arrangement that when the basic ground-plan reaches full development in the andrœcium, i.e. when both whorls are present and complete, they are superposed, for both would be antesepalous (see below under *Fevillea*). Furthermore, such an interpretation is disproved by the evidence afforded by occasional exceptional flowers of *Thladiantha dubia* having a hexamerous ground-plan (K 6 C 6 A 6 G 6 + 6) in which the six stamens, which are all single, are antepetalous (unpublished). Carpel whorls almost always trimerous. Only in one or two genera (*Acanthosicyos*, *Cucurbitella*) are they fairly regularly pentamerous though an isomerous gynœceum occurs occasionally in some other genera (e.g.

*Cucumis* and *Cucurbita*); in a few (*e.g.* *Ceratosanthes*, *Anguria*, *Gurania*) they are often dimerous. When isomerous with the outer whorls as in the above-mentioned exceptional hexamerous flower of *Thladiantha* the outer (sterile) carpel whorl is antesepalous, as is to be expected since the stamen bundles are derived from the same trunk cords as the petal midribs. A disc is very generally present lining the base of the flower wall in the ♂ flower, forming a ring round the ovary in the ♀ flower.

Calyx and corolla fused in the basal region. Sepals (above the level of disjunction) generally small, often with commissural marginal veins (*e.g.* *Bryonia dioica* ♂). Corolla almost always actinomorphic, rarely slightly zygomorphic (*e.g.* *Thladiantha*). Petals (above the level of disjunction) free (*e.g.* *Fevillea*, *Trichosanthes*, *Thladiantha*, *Bryonia*, *Citrullus*) or conjoined for a considerable distance (*e.g.* *Cucurbita*). The staminal filaments resulting from duplication of two of the three members present seldom free almost or quite to the base. Consequently all five stamens seldom appear to be equally spaced, or bear separate straight anthers (*Fevillea*). Generally they are unequally spaced, one standing alone and four being disposed in two pairs, the two of a pair standing close together even when completely separate or more often being more or less fused together (most genera). Rarely all five united (*Echinocystis*, *Cyclanthera*). Anthers, like the filaments, either free (*Thladiantha*) or showing all stages of union up to complete fusion (*Cyclanthera*). Rarely straight with longitudinal dehiscence, more often sinuous or coiled. Ovary multi-locular or unilocular according as the fertile carpels extend to the centre or fail to do so. Styles generally connate, seldom distinct (*Fevillea*, *Alsomitra*, *Sicydium*). Stigmas generally three, sometimes six. When three, centred over the fertile carpels ('commissural') in con-

sequence of the halving of the sterile carpels through the opening to the surface of the three arms of the stylar canal in the mid-line of these carpels. Each stigma then corresponds to  $\frac{1}{2} \times 1 \frac{1}{2}$  carpels. When six, those over the fertile carpels distinct from those over the sterile carpels as, *e.g.* in *Ecballium* in which the former are upright and bilobed (as frequently in consolidated carpels), the latter entire and revolute. Fruit often fleshy with a hard skin (gourd type), sometimes berry-like.

♂ Flower. The spacing of the stamens varies from the one extreme in which the filaments and anthers being free diverge from one another, so that all five *appear* to be antesealous, to that in which the twin products of duplication being more or less completely fused the two pairs of stamens as well as the one single stamen remain plainly antepetalous. Intermediate conditions occur when the single stamen, or the two pairs, or all five are seated on diverging lateral branches of the petal midribs and so do not stand directly over the midribs. A gynæceal rudiment, if present, may take the form of separate (generally three) structures (pistillodes), each supplied by a single vascular bundle and each representing a single sterile carpel; or it may consist of a single entire glandular mass of tissue; or, exceptionally, the three rudiments may be dissimilar in the same flower, one or two appearing as reduced carpels and, conversely, two or one as a corresponding number of outgrowths consisting of glandular tissue.

♀ Flower. Antepetalous staminodes present or absent. When present generally originating and disposed like the stamens of the ♂ flower, usually vascular, rarely with anthers (*Benincasa*, *Melothria*, *Sicydium*). Since the staminodal bundles are derived from the trunk cords which also furnish the petal midribs, suppression of the staminodes does not affect the radial position of the carpels.

The strands which become organised into the placental bundles of the fertile carpels turn inwards from the large central cylinder below the level of the loculi, but the midrib bundles of both carpel whorls, as not infrequently in syngonous types, only attain separate existence as the ovary (or style) is about to become disjoined from the flower wall. At this level strands are detached from the systems developed from the ten primary trunk cords. These strands turn inwards. Some supply the disc. Those not thus utilised become organised into sterile carpel midribs standing over the loculi and fertile carpel midribs on the radii of the placental bundles. Exceptionally, the sterile carpel midrib bundles may be organised considerably below this level (*Thladiantha*). Both sets of midrib bundles are prolonged to the stigma level.

In both ♂ and ♀ flowers anastomoses occur between the sepal and petal vascular systems in the basal region where calyx and corolla are fused. Also, as the two whorls become disjoined, a branch system from the sepal midribs usually passes into the free limb of the petal on each side and gives rise to a petal marginal system. In this character Cucurbitaceæ show the same process of incorporation following degeneration, as Primulaceæ and Theophrastaceæ, in which latter Families also the antesepalous staminal whorl is invariably aborted (see earlier in the present Volume under these two Families, Part II, pp. 406 and 401, respectively; also 22, pp. 131-139 with Figs. 1-12), though the detailed vascular pattern differs in certain respects in accordance with the different relations of the perianth whorls in the two hypogynous Families and in the present syngonous Family. In Primulaceæ and Theophrastaceæ, calyx and gamopetalous corolla are distinct from the base up. In these Families the antesepalous staminal vascular component (which persists though the corresponding stamen may not attain separate morphological form) is therefore of necessity detached at the flower base from the trunk cord which also furnishes the sepal midrib. This detached bundle runs up the corolla tube unbranched and then forks below the level at which the petal limbs become free, each branch of the fork providing a marginal system in the petal limb on the corresponding side. In Cucurbitaceæ, in which fusion of the basal regions of calyx and corolla is prolonged

for some distance, branches arise from the corresponding trunk cords in the common basal region considerably below the level at which the petal limbs separate.

Stages in the process of reduction from the basic cucurbitaceous ground-plan are illustrated by the following genera.

*Schizopepon*. ♀.

♂ K 5 C 5 A 0 + 3, giving rise through duplication of two members to five stamens, the two members of each pair being more or less conjoined (1, 1<sub>(2)</sub>, 1<sub>(2)</sub>) G 3, sterile + 3, fertile.

*Fevillea trilobata*. A 'key' genus. Dioecious.

♂ K 5 C 5 A 5 non-vascular antesealous staminodes + 3, antepetalous, giving rise through duplication of two members to five stamens (1, 1<sub>1</sub>, 1<sub>2</sub>), separate from the base and as they diverge becoming more equally spaced, hence very commonly, though erroneously, described as antesealous G 0.

♀ Insufficiently known.

*Acanthosicyos horrida*. Dioecious.

♂ K 5 C 5 A 0 + 3, giving rise through duplication of two members to five stamens, separate after exertion as in *Fevillea* (1, 1<sub>1</sub>, 1<sub>2</sub>), or more or less united as in *Schizopepon* (1, 1<sub>(2)</sub>, 1<sub>(2)</sub>) (see above), G 0.

♀ K 5 C 5 A 0 + 3, giving rise through duplication of two members to five staminodes, one single, four separate in two pairs (1, 1<sub>1</sub>, 1<sub>2</sub>) G 5 (or 3), sterile + 5 (or 3), fertile.

*Thladiantha dubia*. Dioecious.

♂ K 5 C 5 A 0 + 3, giving rise through duplication of two members to five stamens, one single, four separate in two pairs (1, 1<sub>1</sub>, 1<sub>2</sub>) G a vascular, glandular rudiment.

♀ K 5 C 5 A 0 + 3, giving rise through duplication of two members to five staminodes, one single, four separate in two pairs (1, 1<sub>1</sub>, 1<sub>2</sub>) G 3, sterile + 3, fertile.

*Trichosanthes Anguina*.

♂ K 5 C 5 A 0 + 3, giving rise through duplication of two members to five stamens, one single, four conjoined in two pairs (1, 1<sub>(2)</sub>, 1<sub>(2)</sub>) G 3, rudimentary, sterile + 0.

♀ K 5 C 5 A 0 + 3 simple staminodes G 3, sterile + 3, fertile.

*Benincasa hispida*. Monœcious.

♂ K 5 C 5 A 0 + 3, giving rise as in *Trichosanthes* (see above) through duplication of two members to five stamens,

four being conjoined in two pairs ( $I, I_{(2)}, I_{(2)}$ ) G a vascular glandular rudiment.

♀ K 5 C 5 A 0 + 3 staminodes, one single smaller, two larger double, sometimes with anthers G 3, sterile + 3, fertile.

*Cucumis, Cucurbita.* Monœcious.

♂ K 5 C 5 A 0 + 3, giving rise as in *Trichosanthes* (see above) through duplication of two members to five stamens, four being conjoined in two pairs ( $I, I_{(2)}, I_{(2)}$ ) G represented by rudiments of various forms.

♀ K 5 C 5 A 0 + 3 staminodes, one smaller, two larger. G 3 (or 4 or 5), sterile + 3 (or 4 or 5), fertile.

Most genera

♂ K 5 C 5 A 0 + 3 ( $I, I_{(2)}, I_{(2)}$ ) and G as in *Cucumis* and *Cucurbita* (see above).

♀ K 5 C 5 A 0 + 3 staminodes as in *Cucumis* and *Cucurbita* G constantly 3, sterile + 3, fertile.

*Anguria.* Diœcious or monœcious.

♂ K 5 C 5 A 0 + 2, giving rise through duplication of both members to four stamens conjoined in two pairs ( $I_{(2)}, I_{(2)}$ ) G 0.

♀ K 5 C 5 A 0 + 2 staminodes G 2, sterile + 2, fertile.

*Gurania.* Monœcious or diœcious.

♂ K 5 C 5 A 0 + 2 as in *Anguria* (see above) G 0.

♀ K 5 C 5 A 0 + 0 G 2, sterile + 2, fertile.

## ILLUSTRATIVE TYPES

**\*Bryonia dioica** (Common Bryony). The only British representative of the Family. Diœcious.

♂ K 5 (with well-developed commissural marginal veins) C 5 A 0 + 3, one single, two double through duplication (=  $I, I_{(2)}, I_{(2)}$ ) G 0.

The staminal component of the two petal-stamen trunk cords which supply the double stamens becomes halved when the petal component of these cords turns outwards to become the petal midrib.

♀ K 5 C 5 A, one single, two double staminodes G 3, sterile + 3, fertile. Style single below, three-armed

above, the arms standing over the fertile carpels, each ending in a 'commissural' bilobed stigma. Surmounting the ovary a short cylindrical column formed of the perianth whorls and style not yet disjoined. Fruit a berry.

Staminodes with vascular bundles derived as in the andrœcium of the ♂. Sterile and fertile carpel midrib bundles distinct in the style.

The following genera offer favourable material for the observation of particular features.

**Ecballium Elaterium** (Squirting Cucumber). A 'key' genus. Monœcious.

♂ Stamens as in *Bryonia* (see above).

♀ Staminodes and carpels as in *Bryonia*. Style completely free from the perianth. Stigmas 6, three U-shaped, erect, over the fertile carpels, three horizontal, revolute, over the sterile carpels. This stigma character, which is rare, affords evidence from outward form of the presence of two sets of carpels. For another instance in which stigmas are borne by both sets of carpels, not only when the styles are distinct but also when, as in *Ecballium*, they are connate, see those cited earlier in the present Volume under Ericaceæ, Part II, pp. 397† and 398.

The two vascular bundles for the double stamens of the ♂ and for the double staminodes of the ♀ are furnished by a pair of lateral veins from the corresponding petal-stamen trunk cords, hence the double stamens and staminodes stand symmetrically in front of the corresponding petals. The bundle for the single stamen of the ♂ and for the single staminode of the ♀ is furnished by one lateral vein from the corresponding petal-stamen trunk cord, hence the single stamen and staminode lie to one side of the mid-line of the corresponding petal and give the illusory appearance that they are antesealous.

A similar derivation of the vascular bundles of pairs of stamens (or staminodes) resulting from duplication (or higher multiplication) of the antepetalous staminal members is characteristic of some *Prunus* spp. (Rosaceæ) and in *Corylopsis* (Hamamelidaceæ) (see under these Families earlier in the present Volume, Part 5, pp. 177 and 163, respectively) where, as in Cucurbitaceæ, these paired stamens are epipetalous. Duplication of the antepetalous staminal members accompanied by halving of the staminal component of the corresponding petal-stamen trunk cords below the level of exsertion of the perianth and while these cords are still traversing cortical tissue of the axis on their way to the exsertion level also occurs in the following hypogynous forms: *Peganum* *Harmala* (Zygophyllaceæ), *Hypseocharis* (Oxalidaceæ) and *Monsonia* and *Sarcocaulon* (Geraniaceæ) (for the references to these Families which are treated in Vol. I, see under Hamamelidaceæ, *loc. cit.*). But whereas in the several Families cited above the antepetalous staminal whorl is complete and actinomorphic, every member being duplicated, in the Cucurbitaceæ two of the five members of this whorl are entirely suppressed. In this asymmetric development of the andrœcium the Cucurbitaceæ stand alone.

**Cucumis** spp. (e.g. *C. prophetarum*).

♂ Stamens as in *Bryonia* (see above).

♀ Staminodes and carpels as in *Bryonia*.

The vascular bundles for the double stamens and staminodes are derived as in *Ecballium* (see above), but the bundle for the single stamen and the single staminode is furnished by a lateral branch from a primary lateral of the corresponding petal-stamen trunk cord, hence the asymmetrical relation of these members to the corresponding petal is even more pronounced than in *Ecballium*. The origin and relations of the disc vascular system and of the style vascular bundles are particularly clear in the simple scheme of such small-flowered species as the one cited above.



Of the stigmas two are paired and larger, one unpaired and smaller, an inequality suggestive of a preliminary stage towards reduction to  $G\ 2 + 2$ .

***Thladiantha dubia*.** Diœcious.

Perianth slightly zygomorphic in both ♂ and ♀.

♂ Stamens separate, one single, four approximated in two pairs.

♀ Stamines as the stamens in the ♂.

The sterile carpel midribs are particularly distinct, they and the fertile carpel bundles being organised at different levels. Two are larger, the third much smaller, an inequality suggestive of a preliminary stage towards reduction to  $G\ 2 + 2$  (see also above under *Cucumis*).

***Trichosanthes Anguina*.**

♂ Stamens as in *Bryonia* (see above).

The vascular bundles which serve both the single and the double stamens remain in line with the petal midrib bundles from which they separate, hence the original antepetalous relation of the stamens is readily traceable. Gynœceum represented by three separate monocarpellary pistillodes.

♀ Stamines and style as in *Bryonia* (see above).

The position of the vascular bundles of the staminodes in relation to the petal midrib bundles is the same as that of the bundles of the stamens in the ♂. Disjunction of the style from the surrounding perianth-staminode wall occurs first in line with the fertile carpels, but the sterile carpels remain continuous with the flower wall on the corresponding radii until disjunction of the outer whorls takes place.

## 165. CAMPANULACEÆ

Flower generally ♂, only very exceptionally unisexual through abortion (*Lobelia spp.*, *Pratia spp.*), actinomorphic or zygomorphic, generally completely syngonous, rarely hypogynous (*Cyananthus*) or partially syngonous (e.g. *Platycodon*); in a few forms (in *Cyananthus* and *Platycodon* regularly, in some *Campanula spp.* occasionally) isomerous and pentamerous throughout (K 5 C 5 A 5 G 5, sterile + 5, fertile), more often with a reduced gynæceum (G 3, sterile + 3, fertile or G 2, sterile + 2, fertile), rarely 7-10-merous throughout (*Michauxia*). Corolla rarely divided to the base (*Phyteuma spp.*). Stamens sometimes with broad flattened filaments and then supplied with a much-branched vascular system, a rare condition (*Platycodon*, *Campanula*). A disc with numerous vascular strands generally present. Ovary with 2-10 loculi according to the number of carpels in the whorl, sometimes becoming unilocular above as the central parenchyma comes to an end and the fertile carpels become free on their inner face. Style single, dividing above into as many stigmatic rays as there are sterile carpels, the rays standing in line with these carpels and hence over the loculi. Fruit generally a capsule opening in various ways, rarely baccate (*Pratia*).

Several genera in the Family (e.g. *Campanula*, *Platycodon*, *Lobelia*) include species with forms in which the corolla has undergone multiplication, being represented by 2-5 whorls.

A configuration which appears to present some difficulty is the different orientation of the gynæceum in genera with the same floral formula, the sterile carpels alternating with the stamens in the one class and being superposed upon them in the other. The explanation of this anomaly is to

be found in the vascular ground-plan (see under *Campanula* among Illustrative Types).

### ILLUSTRATIVE TYPES

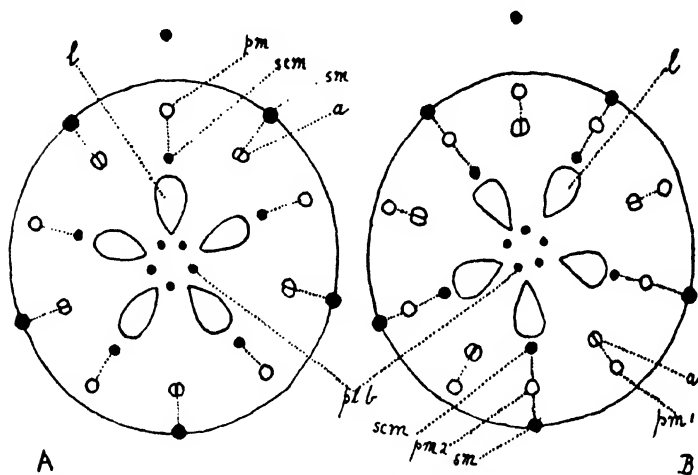
**Cyananthus lobatus.** Flower actinomorphic, hypogynous, pentamerous throughout with all whorls regularly alternating (K 5 C 5 A 5, antesepalous G 5, sterile, antepetalous + 5, fertile, antesepalous); or sometimes with a reduced gynæceum (G 3 + 3 or 2 + 2). Calyx gamosepalous. Staminal filaments not expanded, with a single unbranched vascular bundle. Fruit a capsule with loculicidal dehiscence.

The vascular ground-plan is developed on ten equidistant radii from the outset. Ten trunk cords turn out from the central cylinder on the perianth radii at the flower base, leaving in the centre residual elements which are later organised into the placental bundles of the fertile carpels. The flower being hypogynous, resolution of these cords into their components takes place at once. Those on the sepal radii furnish the sepal midrib and stamen bundles, those on the petal radii the petal and sterile carpel midribs. The fertile carpels are without corresponding midrib bundles. As the ovary passes into the style the placental bundles come to an end, hence each stigmatic ray receives only the midrib of a sterile carpel.

**Platycodon grandiflorum (a).** Type (Fig. 31 A). Corolla single. Flower actinomorphic, partially syngonous, pentamerous throughout with all whorls regularly alternating and orientated as in *Cyananthus* (see above). Sepals free. Staminal filaments broad and flattened with numerous vascular strands. Fruit a capsule dehiscing loculicidally in the upper free region.

The vascular ground-plan resembles that of *Cyananthus* (see above) in the almost simultaneous formation of ten trunk cords at the flower base, the residual elements left in the centre being organised later into the placental bundles of the fertile carpels. Resolution of the trunk cords and alternation of the whorls also follow as in *Cyananthus*, but the flower being syngonous in the lower half the break-up of the cords

occurs here rather later than in the latter type. The fertile carpel vascular bundles sometimes come to an end at the style base as in *Cyananthus*. Sometimes the system of each of these carpels becomes 'condensed' near the top of the ovary into a single bundle corresponding with the midrib bundle of the sterile members. This bundle then also continues up the style, dividing in half below the level of the stigmatic rays so that each ray receives three bundles, a sterile carpel midrib and half the vascular system of the fertile carpel on each side, thus representing  $\frac{1}{2} \times 1 \frac{1}{2}$  carpels.



*Platycodon grandiflorum*. Floral diagrams. A, of the type, corolla single. B, of the variety with a double corolla.

a stamen bundle, l loculus, pl b placental bundle, p m petal midrib bundle, p m 1, p m 2 petal midrib bundles of the outer and inner corolla, respectively, s c m sterile carpel midrib bundle, s m sepal midrib bundle.

FIGURE 31.

(b) **Garden form** with two alternating corolla whorls (Fig. 31 B). The formation of the ten primary trunk cords and of the placental bundles of the fertile carpels takes place as in the type form, but the interpolation of a second, inner corolla alternating with the outer one naturally (in the above circumstances) results in a shifting to the other set of radii of each later whorl. The midrib bundles of the inner whorl of petals, in accord with the ordinary scheme of alternation, alternate with those of the outer petals, hence the stamen bundles, alternating with those of the inner petals, will now

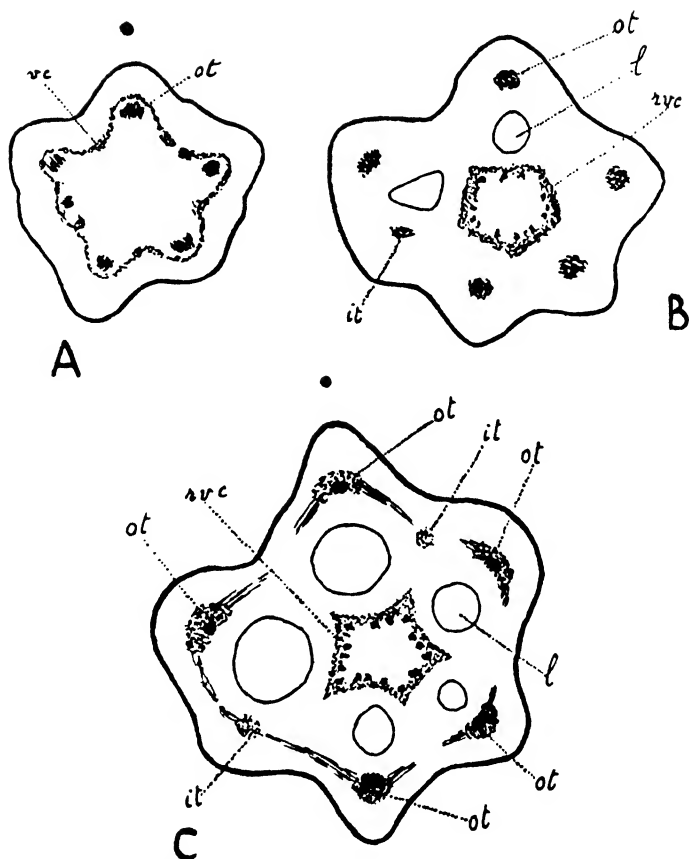
be components of the trunk cords on the petal radii. The sterile carpels in accordance with expectation (and contrary to current descriptions) alternate with the stamens, their bundles being now components of the trunk cords on the sepal radii.

**\*Campanula.** Flower more or less syngonous, actinomorphic. Typically K 5 C 5 A 5, antesealous G 3, sterile + 3, fertile but sometimes, regularly or exceptionally, with G 5, sterile + 5, fertile, and then with the sterile carpels superposed upon the stamens. Sepals free or more or less conjoined. Staminal filaments broad, flattened with numerous vascular strands due to branching. Style and stigmas as in *Platycodon* (see above). Fruit a capsule opening in completely syngonous species by pores at the base or apex through rupture of the tissues between the ribs (trunk cords); or in partially syngonous species by longitudinal slits in the free region of the ovary.

(a) **C. phytidocalyx** (Fig. 32) having regularly, **\*C. medium** (and other *spp.*) having occasionally flowers with G 5 + 5.

The vascular ground-plan differs from that of *Cyananthus* and *Platycodon* (see above) in that only five cords closely followed by a sixth turn outwards at the flower base, leaving behind in the centre the elements which are later organised into the placental bundles. The five cords lie on the sepal radii, the sixth takes up its position on a petal radius. The remaining four antepetalous cords are not organised till much later from anastomosing branches derived from the antesealous cords. The break-up of these ten cords into their components naturally takes place first in those which were organised first, and the flower being completely syngonous the successive whorls of components are detached from the inner face. Hence the first whorl of midrib bundles to be detached will be components of the sepal cords and they are those of the innermost whorl served by these cords, *viz.* those of the sterile carpels. That the stamen bundles should somewhat later be detached from these same cords also follows naturally from the late organisation of the petal cords.

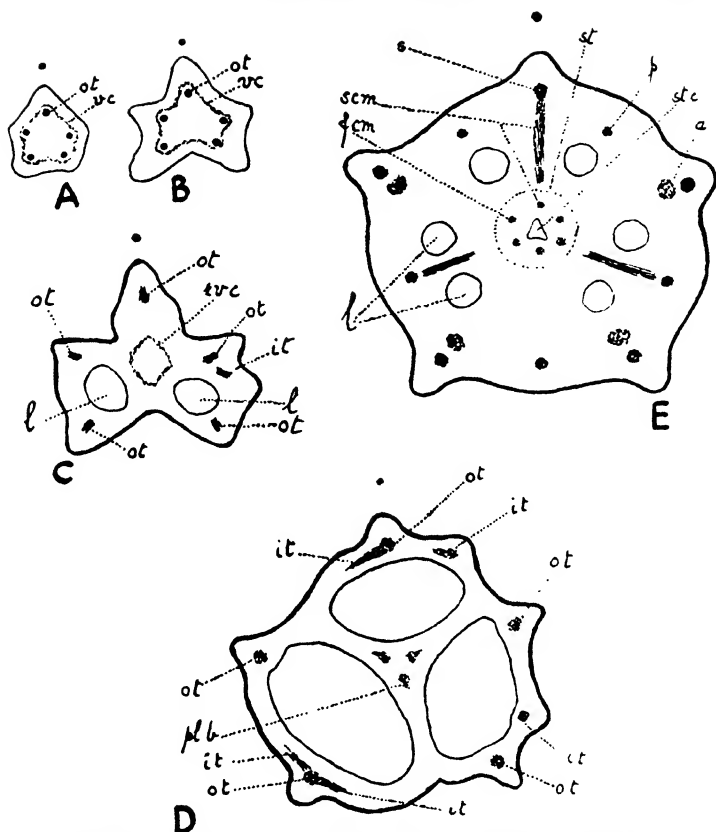
(b) **British spp. and others** (*e.g.* **C. garganica**, Fig. 33) having flowers with G 3 + 3.



*Campanula phytidocalyx*. K 5 C 5 A 5 G 5 + 5. Transverse sections of the flower. A, at a level below the loculi at which the first formed vascular cords have been organised on the five sepal radii. B, at a slightly higher level. A branch has been given off from one of the cords seen in A which runs horizontally towards the adjacent petal radius preparatory to the construction on this radius of one of the later formed cords on the five petal radii. Two of the five loculi have made their appearance. C, at a still higher level at which the later formed five cords on the petal radii are in process of formation at the junction points of horizontal branches from each of the cords on the five sepal radii. The three remaining loculi have made their appearance.

it inner (antepetalous) trunk cords, l locus, ot outer (antesepalous) trunk cords, rvc residual vascular cylinder, vc vascular cylinder.

FIGURE 32.



*Campanula garganica*. K 5 C 5 A 5 G 3 + 3. Transverse sections of the flower. A, from a level slightly lower than that shown in Fig. 32 A. B, from a level between those shown in Figs. 32 A and B. C, from about the same level as that shown in Fig. 32 B. D, from a slightly higher level. The vascular cords on the petal radli are in process of formation directly from horizontally running branches given off by three of the earlier formed cords on the sepal radli. Two of these latter cords give off a branch on each side, one gives off a branch on one side only, the other two remain unbranched. In the centre the placental bundles of the three fertile carpels. E, from near the top of the ovary. The loculi are divided into two cavities through the turning inwards of the sterile carpel midrib bundles which are in process of being detached from one of the cords on the sepal radli and from two of those on the petal radli. Four of the stamen bundles have been detached from the corresponding trunk cords on the sepal radli. The separation of the bundle of the remaining stamen from the posterior sepal cord is delayed since a sterile carpel midrib has first to be detached from this cord. In the centre within the boundary of the (now defined) style column and around the stylar canal the bundles of the three sterile and the three fertile carpels.  
 a stamen bundle, fcm fertile carpel midrib, it inner (antepetalous) trunk cords, l loculus, ot outer (antisepalous) trunk cords, p petal midrib bundle, plb placental bundle, rvc residual vascular cylinder, s sepal midrib bundle, scm sterile carpel midrib, st style tissue, stc stylar canal, vc vascular cylinder.

FIGURE 33.

The vascular ground-plan of  $G\ 3 + 3$  flowers is more 'condensed' and asymmetrical than that of the  $G\ 5 + 5$  flowers. Although, as in these latter flowers, five vascular units and then a sixth are commonly first delimited, the composition of these five original units is not uniform. Very commonly the ten perianth cords to which they give rise are formed in the following way. Two of the five units furnish sepal midribs; two furnish both a sepal and a petal midrib, while the fifth gives rise to one sepal and two petal midribs. The sixth unit furnishes the remaining petal midrib. These relations are illustrated in Fig. 33. As the original units break up the resulting cords diverge so that eventually the ten cords are distributed on equidistant radii. The stamen bundles as in the  $G\ 5 + 5$  flowers are detached from the sepal cords. The sterile carpel midribs are generally spaced as evenly as their derivation from three of the trunk cords permits, one being derived from the trunk cord supplying the posterior sepal and the two others from the two cords supplying the two antero-lateral petals. A sterile carpel midrib having to be detached from one of the cords on the sepal radii causes the separation of the bundle for the stamen on this radius to be delayed so that it does not arise simultaneously with the bundles for the four other stamens. As in general in syngonous types with pentamerous perianth whorls and a trimerous gynæceum, restriction of the two kinds of carpels to the two sets of construction radii, respectively, is abandoned (see *e.g.* under Saxifragaceæ earlier in the present Volume, Part 5, pp. 144, 145). Occasionally, however, all three carpels stand unequally spaced on sepal radii.

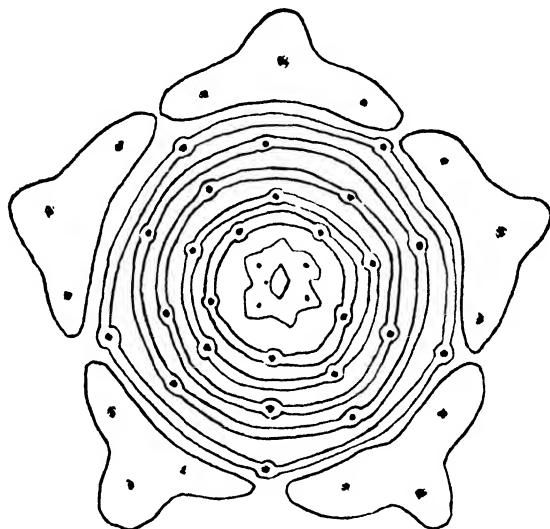
(c) **Garden forms** with 2-5 alternating corolla whorls, two whorls being sometimes formed in *C. medium* (in which the number of carpels in the whorls also ranges up to five) and as many as five whorls in *C. haylodgensis* (Fig. 34).

Here, as in single syngonous forms, the sterile carpel midribs are the first bundles to be detached from the inner face of the trunk cords, consequently their position, which varies in accordance with the number present, is unaffected by the number of corolla midrib bundles subsequently detached alternately from the inner face of the original petal and sepal trunk cords.

**\*Lobelia.** Flower generally completely, sometimes only partially, syngonous, zygomorphic, becoming resupinate



(inverted) through twisting of the pedicel. K 5 C 5 A 5, antesepalous G 2, median, sterile + 2, lateral, fertile. Ovary bilocular. Style single. Stigmas 2, centred over the sterile carpels. Fruit a capsule, opening loculicidally at the top. Multiplication of the corolla occurs in some forms of *L. Erinus*.



*Campanula haylodgensis*. Double variety with five alternating corollas. In the centre an aborted structure representing the androecium and gynoecium.

FIGURE 34.

**L. Erinus** (a). Type (Fig. 35 A). (See description of the genus.) The flower becomes resupinate through torsion of the flower stalk as in some Orchidaceæ (see under that Family, Vol. I, Part 3, p. 92).

The vascular ground-plan, like that of *Campanula*, usually shows some 'condensation' at the flower base. Very generally only eight trunk cords turn outwards originally from the central cylinder, residual vascular elements being left behind in the centre which later became organised, as in the preceding

types, into the two placental bundles. Two of the original eight cords, those standing in the lateral plane, are double, both shortly becoming resolved into a sepal and a petal cord, thus bringing the whole number of cords up to ten. The divergence of the newly separated cords necessary to bring about equal spacing causes the two lateral partitions formed of the two fertile carpels which have no separate midrib bundle to come to lie in line with the interval between two perianth cords instead of remaining in line with two opposite cords. The stamen bundles, as in the preceding types, are detached from the sepal cords, the two sterile carpel midribs from one sepal and one petal cord, the organisation and separation of a carpel midrib from one of the sepal cords delaying the separation of the stamen bundle on this radius as similarly happens in species of *Campanula* with  $G\ 3 + 3$ . Here, as in types with  $G\ 3 + 3$ , the restriction of the two kinds of carpels to the two sets of radii, respectively, is abandoned (see above under *Campanula*). Only the sterile carpel bundles continue up the style into the stigmas, but in some allied genera (e.g. *Centropogon*) the placental bundles are also prolonged so that each stigma then receives the midrib of a sterile carpel and half the vascular system of the fertile carpel on each side.

(b) **Garden form** with two corollas (Fig. 35 B). The whorls regularly alternate as in the similar form of *Platycodon* (see above), the bundles of the inner corolla whorl being detached from the cords on the sepal radii and those of the stamens from the cords on the petal radii.

The areas of different colour and the ciliated regions of the petal margins occur in the same radial position in the two corollas although since they alternate and the radii of the midribs of the petals in the one coincide with the radii of segmentation in the other the pattern of the zygomorphic

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FIG 35. *Lobelia Erinus*. Vascular ground-plan before resupination of the type (A) and of a variety with a double corolla (B) showing the position and origin of the bundles of the several whorls from eight original trunk cords. The trunk cords on the sepal and petal radii arise separately for the three members of the perianth lying to the front and the three members lying to the back of the flower, but those on the radii of the lateral sepal and petal arise from a common cord on each side, and hence at first lie close together on each side. In the type in which the corolla is single the stamen bundles are detached from the cords on the sepal radii, the bundle for the median stamen being detached later than those for the other stamens since a sterile carpel midrib has first to be detached from this same cord. In the double variety, owing to the presence of a second corolla, the stamen bundles are detached from the trunk cords on the petal radii, the formation of the bundle for the median stamen being delayed as in the type. Three cords lie at first close together in the lateral plane (as compared with two in the type) since these cords furnish an inner petal midrib as well as a sepal and an outer petal midrib.

$\alpha$  stamen bundle,  $\alpha'$  retarded stamen bundle,  $cm$  sepal commissural marginal vein,  $fcm$  fertile carpel midrib,  $l$  locus,  $plb$  placental bundle,  $pm$  petal midrib,  $pm\ l$  petal midrib in the outer corolla,  $pm\ s$  petal midrib in the inner corolla,  $scm$  sterile carpel midrib,  $sm$  sepal midrib.

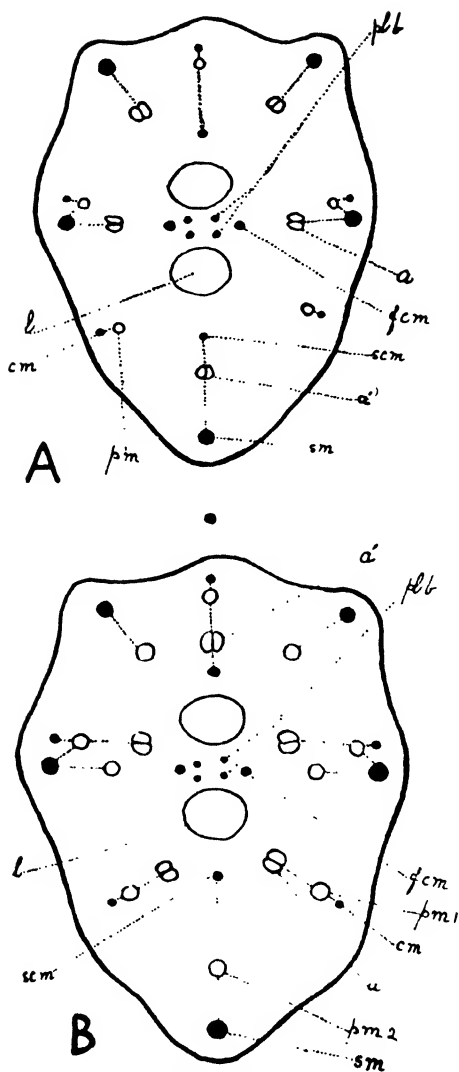


FIGURE 35.

outline is reversed in the two (see 19*b*, p. 216, and 31, p. 138, Figs. 1-4).

(*c*) **Garden form** (Kathleen Mallard) with as many as five or six alternating corolla whorls. Midrib bundles for the additional whorls, as in *Campanula haylodgensis* (see above), are detached successively and alternately from the inner face of the cords on the two sets of radii. Androecium and gynæceum are generally wanting.

## 166. GOODENIACEÆ

Flower ♂, generally zygomorphic and more or less syngonous. K 5 C 5 A 5 (sometimes K 4 C 4 A 4) G (generally) 2, median, sterile + 2, lateral, fertile. Ovary bilocular throughout, or becoming unilocular as the fertile carpels fail to reach the centre, or unilocular throughout. Style single, undivided or forked at the top into as many branches as there are sterile carpels. Stigma unique in form appearing to be enveloped in a structure (the 'indusium') which is sometimes regularly cup-shaped, sometimes bilabiate with equal or with unequal lips. Ovules generally numerous, in several rows on each placenta, rarely one or two in each loculus. Fruit generally a capsule, dehiscing only septicidally or both septicidally and loculicidally through median splitting of both fertile and sterile carpels, sometimes drupaceous or nut-like and indehiscent.

At the flower base of the pentamerous type ten vascular cords on equidistant radii supply the bundles of the sepals, petals, stamens and sterile carpels. The residual vascular elements left in the centre become differentiated into the placental bundles of the fertile carpels which are without midrib bundles. The trunk cords on the five sepal radii furnish the sepal midribs which form true lateral veins, commissural lateral veins to the petals—a development only occurring elsewhere among syngonous types with an antesealous andrœcium in Calyceraceæ and Compositæ (see under these Families later in the present Volume, Part 14, pp. 512 and 516, respectively)—and the stamen bundles. In pentamerous types with a dimerous gynœceum the anterior trunk cord also furnishes the anterior sterile carpel midrib. Similarly the posterior cord on a petal radius provides the posterior sterile carpel midrib as well as the posterior petal midrib. The four cords on the other petal radii remain entire and become the midribs of the four other petals. Thus the whole vascular system exhibits a diagrammatic regularity in contrast with that of most Compositæ. For in the completely syngonous flowers of this latter Family extreme reduction has resulted in most types in the loss of both sepal and petal midribs with consequent restriction of

those vascular bundles present above the summit of the ovary, *viz.* the petal commissural laterals and stamen bundles to one set of radii (the radii of the sepals). While below the exertion level the vascular system of some types is 'condensed' into only two trunk cords (see later under *Compositæ*, *loc. cit.*, p. 516).

The peculiar features of the stigmas arise from the difference in form of the ends of the sterile and of the fertile carpels, their unequal length and the more or less complete encirclement of the two latter by the two former. When the style forks into two branches (as generally in *Calogyne*) each of the two indusial 'cups' is open down the ventral face. For as the result of forking each cup is constructed of  $\frac{1}{2} \times 1 \frac{1}{2}$  carpels, *i.e.* of one whole sterile carpel which incompletely enwraps half of the stigma of the fertile carpel on each side which has become split in two. In one species (*C. pilosa*) an intervening third fork is sometimes developed with a flattened, straight-sided indusium open at both sides. The ovary is then unilocular with an incomplete or rudimentary septum. This construction is explicable on the supposition that the gynæceum of such flowers is tetramerous having a ground-plan of 4 orthogonal sterile carpels + 4 diagonal fertile carpels. The two indusial 'cups' open only on the ventral face will then, as in flowers with a dimerous gynæceum, consist of a whole median sterile carpel + half the stigma of the split fertile carpel on each side ( $\frac{1}{2} \times 1 \frac{1}{2}$ ), while the unpaired third cup which is open back and front is formed of the two lateral sterile carpels + the remaining halves of the four diagonal fertile carpels ( $1 \frac{1}{2} \times 1$ ).

In the dimerous gynæceum of all genera only the two midrib bundles of the sterile carpels are prolonged into the style. Continuing to the top they there give rise to the richly branched system in the lip(s) of the indusial cup.

### ILLUSTRATIVE TYPES

**Goodenia, Leschenaultia.** Flower syngonous. K 5 C 5 A 5 G 2, median, sterile + 2, lateral, fertile. Style undivided. Indusium bilabiate. Ovules numerous. Fruit a capsule, dehiscing into two or four valves.

**Selliera.** Flower as in *Goodenia* (see above). Fruit more or less fleshy, indehiscent.

**Scævola spp.** Flower as in *Goodenia* (see above), but the 'indusium' cup-shaped and ovules 1 or 2. Fruit indehiscent.

## 167. STYLIDIACEÆ (CANDOLLEACEÆ)

Flowers generally ♂ and zygomorphic, rarely unisexual by abortion or actinomorphic, syngonous. Sepals generally 5, free or forming two lips. Petals generally 5, equal or the anterior smaller (= labellum). Stamens 2 postero-lateral, united throughout with the single style. Gynæceum of 4 carpels, 2 median, sterile, 2 lateral, fertile. Ovary bilocular, becoming unilocular above as the fertile carpels cease to extend to the centre, only exceptionally unilocular throughout through non-development of the second loculus. Stigma terminal, bilobed with the lobes centred over the sterile carpels or entire. Ovules numerous. Fruit capsuloid, dehiscent or indehiscent.

## ILLUSTRATIVE TYPES

**Stylidium.** Calyx bilabiate. Stigma entire.

**S. graminifolium.** Ovary bilocular. Stigma oval, centred symmetrically between the anthers.

Apart from the placental vascular bundles which are situated in the centre of the partition the carpels are without independent bundles even in the region of the style and stigma, the stamen-style column receiving only the two staminal bundles.

**S. adnatum.** Ovary unilocular through non-development of the posterior loculus. Stigma asymmetrical and excentric.

## 168. CALYCERACEÆ

Inflorescence a capitulum surrounded by an involucre of bracts. Flowers all ♂ or those at the periphery ♂, those in the centre ♀ with a rudimentary gynæceum (*Acicarpha*), syngonous, actinomorphic. K 4-6 C 4-6 A 4-6. Filaments monadelphous below. Anthers syngenesious at the base. G 2, 1 sterile, 1 fertile, or, exceptionally, G 3, 2 sterile, 1 fertile. Ovary unilocular. Ovule solitary, pendulous from near the top of the loculus. Style single. Stigma capitate, entire or very slightly bilobed. Fruit achene-like, sometimes compound through the union of those of adjacent flowers.

The vascular system of the flower is exceptionally simple and diagrammatic in its arrangement. In types with a pentamerous perianth and andrœcium it consists at the flower base of two alternating whorls of five cords. Each of these cords on the one set of radii furnishes a sepal midrib (if present), a commissural marginal vein to the petal on either side and a stamen bundle; each of those on the alternate radii furnishes a petal midrib. The presence in the petals of marginal veins of commissural origin in syngonous types with an antesealous stamen whorl is a highly exceptional construction, occurring as a regular feature outside the present Family only in Goodeniaceæ (see earlier in the present Volume, Part 14, p. 509) and in Compositæ (see later in the present Volume, Part 14, p. 516). These veins are detached from the antesealous cords as single bundles which run upwards in the corolla tube, forking just below the level at which the petals separate to provide the marginal vein for the adjacent edge of the petal segment on either side, the bundle for the superposed stamen having been detached below this level. The two carpal bundles are detached below the top of the loculus from the two primary cords standing opposite to one another in the median plane. These two detached bundles are continued directly upwards into the style. They represent the midrib bundles of two median carpels. The funicle bundle is derived from the posterior carpal bundle. This vascular ground-plan clearly indicates a gynæceum of two carpels and makes it possible to state with confidence that also in the closely related Family Compositæ, in which the evidence is less clear, the



number of carpels is 2. When the stigma is entire the number of vascular bundles in the style affords the sole clue to the number of these carpels. In the typical flower in which two bundles are present they are detached from an antesepalous, and the opposite antepetalous trunk cord, respectively. When there are three bundles they arise as symmetrically as the pentamerous ground-plan permits.

### ILLUSTRATIVE TYPES

**Boopis.** Stigma enlarged, entire or very slightly bilobed.

**Acicarpa.** Stigma scarcely enlarged, entire.

## 169. COMPOSITÆ

Inflorescence almost always a many-flowered, rarely a few- to one-flowered capitulum, surrounded by an involucre of bracts and with or without scale-like bracts subtending the individual florets. The florets of a capitulum may all be similar or those at the periphery may differ in form or/and function from those in the centre. The capitula may be classed accordingly under three heads: (1) Discoid when the corolla of all the florets is tubular in form; (2) radiate when the corolla of the central (disc) florets is tubular and that of the peripheral (ray) florets ligulate (strap-shaped); (3) ligulate when the corolla of all the florets is strap-shaped. In the ligulate capitulum all the florets are usually ♂. In the radiate type those of the disc are ♂, those of the ray ♀, either fertile or sterile. In the discoid type all are usually ♀ or those at the periphery are neuter. Florets when ♂ or ♀ syngonous.

Calyx generally in the form of a narrow rim crowning the ovary from which a ring of simple or branched hairs (pappus) is developed, rarely assuming distinct morphological form as teeth or membranous scales, or becoming leafy (some monstrous flowers). Corolla generally pentamerous. When of tubular form usually actinomorphic with five lobes, seldom zygomorphic and more or less two-lipped. When ligulate always zygomorphic, the short basal tube becoming split on the ventral face between the two postero-lateral petals and then flattened out as the strap-shape is assumed. The apex of the flattened limb is entire or 2-5-toothed according as all the petals remain united to the top, or as individual petals or pairs of petals become free at the tips, or as they separate asymmetrically. Stamens 5, alternating with the petals. Filaments conjoined for a longer or shorter distance with the

corolla. Anthers, as they develop, becoming loosely coherent (syngenesious). In the ♀ ray florets of some species (e.g. *Senecio lobatus*, *S. Petasitis* and other species, *Osteospermum moniliferum*) 1-4 non-vascular staminodes are usually present alternating with the petals, sometimes with free barren anthers (*S. Petasitis*). Carpels 2, median, 1 sterile, 1 fertile (see below). Ovary unilocular. Ovule solitary, basal, erect. Style single, forking above into two arms standing in line with the carpels and stigmatic on their inner face.

The not infrequent occurrence in various genera of occasional flowers with more than two stigmas and with a correspondingly increased number of vascular bundles in the undivided region of the style probably indicates that the normally dimerous carpel whorl has arisen by reduction from an originally complete (pentamerous) whorl.

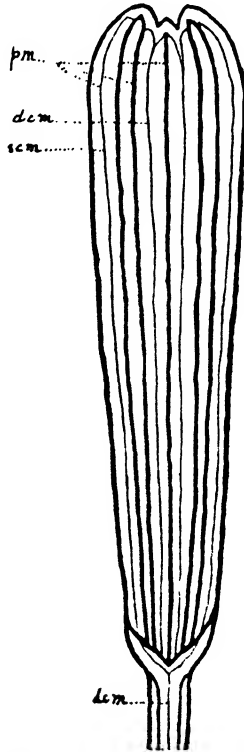
The vascular system presents several unusual features resulting from extreme 'condensation' in some parts of the flower and total loss of portions of the system in other parts. The calyx is ordinarily non-vascular, vascular elements occurring only exceptionally when the sepals are in the form of teeth or scales or in abnormal flowers when they become leafy (occasionally in *Helenium spp.*). A single vascular strand reaches, and sometimes continues as such for a short distance into the flower base. In either case it divides in two below the locus, the bundle serving the solitary ovule being given off immediately from one of these two compound trunk cords. The compound nature of these cords renders it difficult to determine whether the above-mentioned detached bundle should be regarded as a placental strand from one of the two median carpels or as representing the 'condensed' system of an inner fertile carpel whorl of which one member alone survives and comes to an end with the formation of the ovule. But comparison with the nearly related Family Calyceraceæ leaves no doubt that the above-mentioned detached bundle represents a placental strand, and that as in that Family the gynæceum is formed of two carpels, one sterile, one fertile (see under Calyceraceæ earlier in the present Volume, Part 14, p. 512). No separate carpel midrib bundles are present in the region of the ovary. They originate immediately below the style, either directly from the primary trunk cords or from a complex to which these cords give rise at this level, and continue into the stigmas, the number

of bundles in the style filament corresponding with the number of carpels.

In a type in which 'condensation' of the vascular scheme has been carried to the limit as *e.g.* in *Bellis perennis*, the two above-mentioned cords arising below the loculus continue undivided in the wall of the loculus on opposite sides to the top of the ovary. Here each splits up into a group of bundles. One bundle from each group enters the style and runs to one of the two stigmatic arms. The other bundles of the two groups serve the corolla, and in the ♂ floret the andræcium. In the ♀ (disc) floret these bundles are ten in number, two being superposed on each of the five radii alternating with the five petals. This distribution is accounted for by the fact that the corolla shows the unusual feature of possessing petal marginal bundles of commissural origin, while the petal midribs have been lost. Hence it comes about that the five bundles which serve the alternating whorl of stamens are superposed upon these bundles of the corolla. In the ♀ (ray) floret the number of bundles in the limb of the corolla varies generally from two to four according as the two original primary cords, after giving off the two bundles to the style, continue upwards undivided or as one or both break up. The apex of the corolla limb being usually entire in *Bellis*, the evidence regarding the relation of these bundles to the individual petals composing the limb, which, when the limb is 5-toothed, is clear, is here lacking. But comparison of the vascular system of the entire corolla with the complete vascular scheme of those types with a toothed apex leaves no doubt that the bundles in question are marginal veins of commissural origin which have survived after the midrib bundles have been lost, but which themselves are now in process of disappearing. This process is exemplified in many species having a corolla with a toothed apex in which the number of veins is frequently four as the result of the disappearance of the posterior commissural marginal vein as well as the midribs. (This marginal vein is the one that must necessarily fork at the level at which the tube flattens out (see below under *Cineraria*), a necessity which is possibly a main factor in its early loss, for the four persisting veins do not usually fork until the petal segments separate (see Fig. 36).)

In the genus *Senecio* the extent of the degeneration in the vascular system varies considerably. In this genus the primary break-up of the single vascular cord entering the floret into as many bundles as serve the corolla takes place below the level of the loculus. It thus differs from *Bellis*, in that several bundles pass up in the wall of the loculus but, as in *Bellis*, the two bundles for the style are detached from

two of their number at the summit of the ovary. In the corolla of the ray florets of *S. cruentus* (Cineraria) which is generally three-lobed at the apex and which affords one of the rare examples in which midrib bundles still persist, the total number of primary bundles varies but is very generally eight in the short basal tube, becoming nine in the flat limb. Five of the eight bundles are midribs, three are commissural in origin and provide the marginal veins of the lobes. At the



*Senecio cruentus* (Cineraria). Limb and upper part of the tubular portion of the corolla of a ray floret. In the limb which ends in a median single, and two double lateral lobes are the midrib bundles of the five petals. On each side of the middle petal midrib a double (unsplit) commissural marginal vein which splits into its two components at the apex. In the tubular portion a third commissural marginal vein which splits into its two components as the tube opens out.

*p m* petal midrib, *d c m* double (unsplit) commissural marginal vein, *s c m* single (split) commissural marginal vein.

FIGURE 36.

level at which the short tube passes into the flat limb the posterior commissural bundle splits in half, hence the appearance of nine bundles in the limb. One midrib bundle runs to the middle lobe which is the smallest of the three and corresponds to a single petal, two to each of the larger outside lobes which are formed of two completely united petals between which there is no commissural vein. These relations are illustrated in Fig. 36.

In the disc florets the basal break-up of the single entering bundle results in the formation of five bundles which, passing up in the wall of the loculus, give rise at the top to five petal commissural bundles and five superposed stamen bundles, together with the two style bundles, the petal midrib bundles having been lost as in *Bellis*. In *S. vulgaris* (Groundsel), in which only disc florets are present, the corolla is sometimes (? always) non-vascular, the commissural veins having disappeared as well as the petal midribs. Hence the five bundles formed at the basal break-up, after the two bundles for the style have been detached at the top of the ovary, continue upwards as the stamen bundles.

## ILLUSTRATIVE TYPES

### (i) LIGULIFLORÆ

Plants with latex. All florets ligulate. Apex of the corolla limb generally 5-toothed. Petals generally without midribs but with commissural marginal veins.

**\*Taraxacum Dens-leonis** (Dandelion), **\*Sonchus** (Sowthistle), **\*Crepis**, **\*Hieracium** (Hawkweed).

### (ii) TUBULIFLORÆ

Plants without latex, capitula radiate or discoid.

#### (a) Capitula radiate.

**\*Bellis perennis** (Common Daisy). Apex of the corolla of the ray florets entire. (For the vascular scheme see general account of the Family.)

**\*Senecio spp.** (*e.g.* **S. cruentus**, Cineraria), **\*Chrysanthemum leucanthemum** (Ox-eye Daisy). Apex of the corolla of the ray florets 3-toothed. (For the

vascular scheme of *S. cruentus* see general account of the Family and Fig. 36.)

(b) Capitula discoid.

**\*Carduus** (Thistle). Florets all similar and ♂.

**\*Centaurea spp.** (*e.g.* **\*C. Cyanus**, Cornflower, **\*C. nigra**, Knapweed). Outer florets larger than the rest and neuter.





## Part 15

### Monocotyledons

Family	170.	Typhaceæ
„	171.	Sparganiaceæ
„	172.	Pandanaceæ
„	173.	Aponogetonaceæ
„	174.	Potamogetonaceæ
„	175.	Naiadaceæ
„	176.	Scheuzeriaceæ (Juncaginaceæ)
„	177.	Alismataceæ
„	178.	Butomaceæ
„	179.	Hydrocharitaceæ
„	180.	Palmæ
„	181.	Cyclanthaceæ
„	182.	Araceæ
„	183.	Lemnaceæ



## 170. TYPHACEÆ

Marsh or aquatic plants. Inflorescence a long terminal spike. Flowers densely packed, unisexual, without trace of the non-functional sex, ♀ below, ♂ above, those at the top of the spike being generally aborted. Both sexes without perianth, the base of the flower being surrounded by numerous hairs. ♂ Flower. A generally 3, sometimes 2 or 5. ♀ Flowers of two kinds, functional and sterile, mixed together irregularly throughout the lower region of the spike. Gynæceum of 2 carpels (12, pp. 459, 460, and p. 462†). Ovary unilocular. Functional flower. Gynæceum zygomorphic. Ovary borne on a long stipe, elliptical, tapering into a long style which ends in a spoon-shaped expansion, stigmatic on the concave face (a type of zygomorphic (dorsiventral) symmetry common among stigmas formed of a single carpel). Carpels dissimilar, one sterile, prolonged above to form the style and stigma, the other bearing a single ovule pendulous from the top of the loculus and coming to an end at this level. Fruit one-seeded, indehiscent. Sterile flower. Gynæceum actinomorphic. Ovary pear-shaped, much larger than that of the fertile flower, surmounted by a short central spike representing an aborted style without stigma. Carpels similar, both sterile. Loculus empty.

The vascular scheme of the two kinds of ovary is in accord with the character of the component carpels. In the functional ovary the midrib bundle of the sterile carpel continues up into the style, that of the other furnishes the bundle to the ovule and comes to an end at this level. In the sterile ovary both midrib bundles generally cease below the top of the ovary, one usually a little before the other.

### ILLUSTRATIVE TYPES

**\**Typha* spp.** (Bulrush, Reedmace) (*e.g.* **\**T. latifolia***, **\**T. angustifolia***) (12, p. 462, Figs. 1-3). See the characters of the Family.

## 171. SPARGANIACEÆ

Marsh or aquatic plants. Inflorescence of several spherical clusters distributed at intervals in the upper region of the shoot. Flowers unisexual, ♀ in the lower clusters, ♂ in the upper, both without trace of the non-functional sex. Each flower subtended by a bract. ♂ Flower. T 3, bract-like A 3. ♀ Flower, T 3 or 6, bract-like. Gynæceum varying in construction even among the flowers in the same cluster owing to 'twinning' of the axis once, or even twice, within the individual flower, but above the level of the perianth, accompanied by complete fusion of the structures thus produced. Some of the numerous forms which occur are enumerated below (see also 12, pp. 460-465).

- (1) Simple type. Most numerous. Carpels 2, standing opposite to one another, one sterile, one fertile. Ovary unilocular with a single ovule. Style single, centred over the sterile carpel, stigmatic along the inner face.
- (2) Type in which 'twinning' occurs once, the one product of division developing less vigorously than the other. Infrequent. Carpels 3, 2 sterile, 1 fertile, the second fertile member failing to develop. Ovary unilocular with a single ovule. Styles 2, centred over the sterile carpels. Stigmas as in the simple type.
- (3) Type in which 'twinning' occurs once, both products of division developing equally. Very frequent. Carpels 4, 2 sterile, 2 fertile. Ovary bilocular, each locus containing a single ovule. Styles 2, centred over the sterile carpels. Stigmas as in the simple type.

- (4) Exceptional type. Carpel 1, sterile, without loculus or ovule, tapering into a stylar filament.
- (5) Exceptional type in which 'twinning' occurs a second time in one only of the two products of the first division. Carpels 5, two in one half of the gynæceum, three in the other. Of the two in the one half one is sterile and one fertile ; they stand opposite to one another and there is one simple style as in the simple type. Of the three in the other half two are sterile and one fertile as in Type 2, the two sterile being turned sideways to the other half of the gynæceum, and standing nearly but not quite opposite to one another ; there is a single style shank which shortly divides into two.

The construction of the simple gynæceum of *Sparganium* is thus similar to that of *Typha* (see earlier in the present Volume, under Typhaceæ, Part 15, p. 523), but the massive ovary shows a more richly developed vascular system.

#### ILLUSTRATIVE TYPES

**\**Sparganium* spp.** (*e.g.* **\**S. ramosum***, Bur-reed) (12, pp. 460-465, Figs. 4-32). See the characters of the Family.

## 172. PANDANACEÆ

Inflorescence, as in Sparganiaceæ (see earlier in the present Volume, Part 15, p. 524), of dense clusters terminating, or strung along, the end of the stem. Flowers without bracts or bracteoles, unisexual and dioecious, frequently with rudiments of the non-functional sex. Number of floral members variable. Perianth wanting. ♂ Flowers densely crowded; when sessile not clearly delimited from one another, when pedicellate plainly defined, bearing numerous stamens arranged in an umbellate or racemose group. ♀ Flowers delimited by the staminal rudiments when present. Ovary, as in *Sparganium* (*loc. cit.*, p. 524), of a variable number of carpels. Carpels sometimes 2, 1 sterile, 1 fertile, the ovary being unilocular with a single ovule; sometimes  $> 2$ , the ovary being either unilocular with several ovules or multilocular with one ovule in each loculus. Stigma sessile or nearly so. Fruit a berry, or compound consisting of several drupaceous individual fruits (syncarp), with a persistent short hard style base.

## ILLUSTRATIVE TYPES

**Freycinetia.** Ovary of many carpels, unilocular, with many ovules. Fruit a berry.

**Pandanus** (e.g. *P. utilis*, Screw-Pine). Ovary of two to several carpels. Ovules solitary in each loculus. Each fruit drupaceous.

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FIG. 37. *Pandanus parvus*. A. Preparation of a portion of the axis with the lower part of the attached gynæceum of a ♀ flower showing the vascular plexus below the flower from which numerous strands pass upwards into the wall of the bicarpellary ovary and a single strand to the funicle of the solitary ovule. B-G. Transverse sections of the gynæceum taken at successively higher levels. B. Showing the numerous vascular bundles in the short stipe and in the ventral mid-line, the bundle from which the strand to the funicle is derived. C. Showing in the centre the strand for the funicle cut obliquely. D. After the appearance of the loculus into which the ovule projects. E. After the loculus has closed giving place to a small stylar canal. Between the canal and the ventral surface a tract of glandular cells. F. The tract of glandular cells seen in E now appears as a 'sepal' gland with lumen. To the right part of the outline of a contiguous gynæceum. G. The 'sepal' gland has extended to the surface, giving rise in its peripheral portion to a radial split in the mid-line of the fertile carpel.

*f b* funicle bundle, *g t* glandular tract of cells, *l* loculus, *o* ovule, *p x* plexus of vascular strands in the axis below the flower, *s c* stylar canal, *s g* 'sepal' gland.

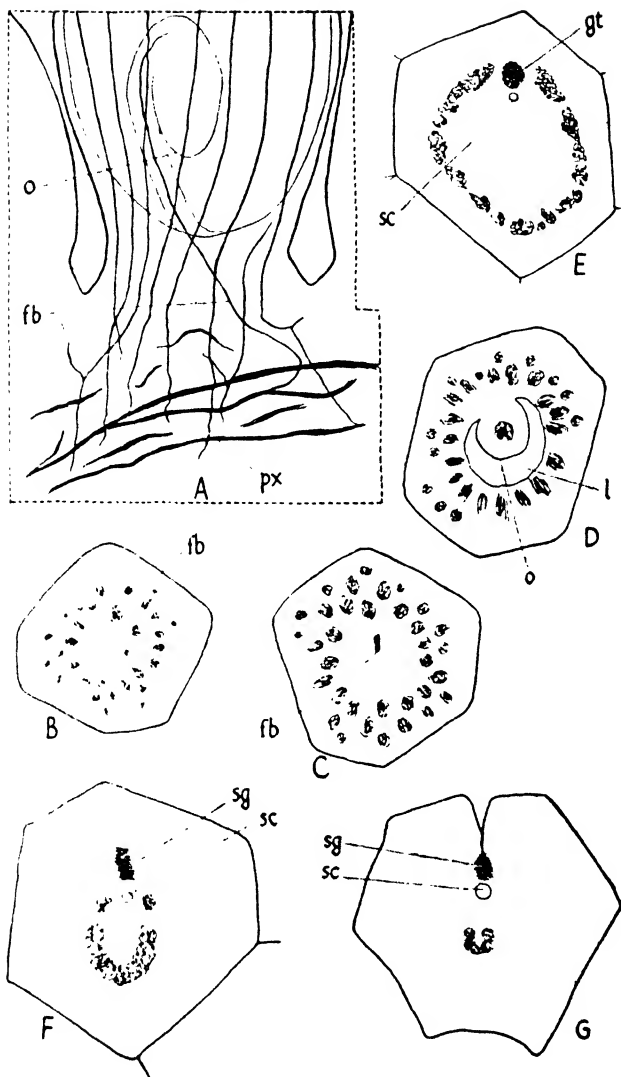


FIGURE 37.

The single massive ovary is furnished with a large number of vascular bundles derived from more than one point in the underlying axial vascular plexus and arranged in a ring. In the lower portion of the ovary the limits of the vascular systems of the sterile and of the fertile carpel are not obvious but above the ovule level, as the loculus begins to close, the residual cylinder breaks across in the same way as in many Leguminosæ (see under that Family, earlier in the present Volume, Part 5, p. 187). The strands in the larger portion become aggregated into a single stout cord, the midrib of the sterile carpel; the smaller portion consists of the twin bundles of the fertile carpel. Both sterile and fertile bundles are continued to the level at which the styler canal opens to the surface by an extension of the septal gland in the mid-line of the fertile carpel.



## 173. APONOGETONACEÆ

Aquatic plants. Inflorescence a simple or 2-5-forked, long-stalked spike projecting above the surface of the water. Flowers ♂ or very rarely diœcious, actinomorphic, hypogynous. T 3 or more often through suppression 2. A generally 3 + 3 but sometimes as many as 17 distributed irregularly in 3-4 series. Gynæceum apocarpous except in *Aponogeton distachyus*. Carpels generally 3, sometimes 4 or 5 ; in unisexual flowers 6-8 ; in apocarpous types in one whorl. Ovaries monocarpellary. Ovules in two series. Analysis of the gynæceum of *A. distachyus* presents some difficulty owing to the presence of a central vascular plexus at the level of origin of the carpels and to the complexity introduced into the ground-plan by the formation of numerous stamens. Inasmuch as the ovules which are crowded together at the base of the ovaries appear, at least sometimes, to arise more than two abreast ; and as vascular strands extending outwards from the central plexus in the side walls of the ovary give rise to a vascular system separate from that derived from the midrib ; and, finally, as the ovaries are not free from one another at the extreme base the balance of evidence points to a pseudo-apocarpous gynæceum in which the ovaries as they become free consist of one sterile carpel and half the fertile carpel on each side through early median radial splitting of these latter carpels from without inwards (12, pp. 469-472†).

## ILLUSTRATIVE TYPES

**Aponogeton (Ouvirandra) fenestralis** (Lace-leaf Plant). T 2. A 3 + 3 G 3 apocarpous. Ovaries monocarpellary. Ovules in two series.

**A. distachyus** (Cape Pondweed) (12, pp. 470, 471, Figs. 51-54). T 1 (in terminal flowers commonly 2) A 6-12 or more G 3 or 2 or 5 sterile + (?) 3 or 2 or 5 fertile, pseudo-apocarpous (see account of the Family).

## 174. POTAMOGETONACEÆ

Aquatic plants. Flowers ♂ or unisexual and then mostly monœcious, actinomorphic. Perianth when present single, much reduced, hypogynous. Tepals separate (*Potamogeton* (12†), *Posidonia*, *Althenia* ♀ ) or united into a cupule (*Zannichellia*, *Althenia* ♂ ). Stamens 1-4, in ♀ types possessing a perianth superposed upon the tepals and conjoined with them (*Potamogeton*, *Posidonia*). Gynæceum apocarpous and then generally of four monocarpellary ovaries (sometimes more or fewer); or syncarpous, the single unilocular ovary being then formed of 4 or 3 or 2 carpels, of which only one is fertile (see below). Ovule always solitary, generally pendulous from the top of the loculus or from a lower level on the ventral suture in some apocarpous types. Stigmas in apocarpous types single on each ovary, zygomorphic; in syncarpous types generally 2, filamentous. Fruit drupaceous or with a membranous pericarp, one-seeded, indehiscent.

Reduction in the vascular system renders it difficult to determine the number of carpels composing the single ovary in syncarpous types. The presence of two lateral stigmas in conjunction with two median vascular bundles as in *Phyllospadix* (see below under Illustrative Types), and consideration of the number and position of the stigmas in species of *Naias* in the allied Family Naiadaceæ (see later in the present Volume, Part 15, p. 535) support the interpretation of G 4, two median and two lateral, the two lateral carpels being sterile and bearing stigmas, the posterior carpel being of the consolidated type and bearing the ovule on the midrib, the anterior carpel bearing neither stigma nor ovule. On the other hand the approximation of the two stigmas towards the mid-line at the back may indicate that they are formed by the posterior consolidated fertile carpel and that the gynæceum

in such types as *Phyllospadix* and *Zostera* should be represented as G 2, the other carpel being anterior, sterile, and stigmaless.

### ILLUSTRATIVE TYPES

**\*Potamogeton spp.** (Pondweed) (12, p. 465 and p. 470, Figs. 33-37). Inflorescence a many-flowered spike projecting above the surface of the water. Flower ♂. T 4, orthogonal A 4, orthogonal G 4, diagonal (or rarely more), apocarpous. Ovaries monocarpellary. Stigmas sessile.

The vascular bundles for the stamens do not originate independently but turn outwards conjoined with those of the tepals, hence the superposition of the two whorls. The central portion of each of the four trunk cords gives rise to the tepal midrib, the two lateral portions of the cord serve the two half anthers of the superposed stamen which are separated by the basal portion of the tepal. Each carpel (ovary) with midrib bundle; and on the same radius the placental strand derived from it.

**\*Ruppia rostellata.** Inflorescence a two-flowered spike. Flower ♀. T ? 2, median A 2, median G 4, apocarpous, orthogonal. Ovaries monocarpellary, sessile but in the fruiting stage carried up on a long stipe. Stigmas peltate.

The vascular system greatly reduced. The two halves of the anther of each stamen separate and borne on a short, broad flap of tissue without a differentiated vascular bundle from which they are readily detached. Analogy with *Potamogeton* suggests that this tissue represents a reduced tepal separating the two halves of the stamen (see above). Carpels without a midrib bundle. Ovule pendulous from the top of the loculus where the placental strand comes to an end.

**\*Zannichellia palustris** (Horned Pondweed). Flowers unisexual, monœcious, ♂ and ♀ generally close together, terminating their respective axes which are clustered together at the end of a short axillary branch. ♂ Flower. T 0 A 1, sometimes 2. Anther entire. The occasional development of two stamens in the ♂ flower suggests that when only one stamen is present it is not a terminal structure but is the

surviving member of a lateral pair. ♀ Flower. T a membranous non-vascular cupule G (generally) 4, diagonal, apocarpous. Ovaries monocarpellary, styled, with a large oblique, funnel-shaped stigma. Carpels without a midrib bundle. Ovule pendulous from the top of the loculus where the placental strand comes to an end.

**Phyllospadix Torreyi.** Flowers unisexual and diœcious. Inflorescence a spadix (spike with fleshy axis) enclosed in a sheathing bract (spathe). ♂ Flowers in two alternating rows on the spadix, each of one stamen, the two halves of the anther separated by a broad band of tissue (? - reduced tepal separating the two halves of the split stamen, see above under *Ruppia* and *Potamogeton*). ♀ Flowers in two alternating vertical rows on the flattened spadix, each subtended by a bract and consisting of a naked syncarpous gynœceum beside which are a pair of processes regarded as corresponding to the two separated halves of a single anther in a monœcious type such as *Zostera* (see below under Illustrative Types). Carpels 4 or 2 according to which of the two interpretations outlined above in the general account of the Family is adopted. The ovary with two lateral, hollow, horn-like prolongations below and two lateral but approximated filiform stigmas above. Ovary unilocular but with three separate cavities at the extreme base below the level at which the cavity in each horn becomes continuous with the central cavity. Ovule pendulous from the top of the loculus on the ventral face.

A central vascular strand runs up the length of the flattened spadix. Branches from this strand arising at successive intervals alternately to right and left furnish a midrib to the subtending bracts. In the ♀ inflorescence branches from this central strand arising similarly at successive intervals, one to the right and one to the left, run respectively to a staminode and to a gynœceum. Hence these two structures which do not stand at quite the same level are seated on opposite sides of the axial strand, the one alternating with the other in each vertical row. The branch which serves the gynœceum divides into two bundles immediately below the loculus. One of these bundles passes up in the anterior mid-line of the ovary wall and ends blindly, the other which runs up in the posterior mid-line serves the ovule. These two bundles are regarded as the midribs of two median carpels of which only the posterior is fertile (see below under *Zostera*). For the interpretation to be placed on the position of the two stigmas see under the general account of the Family.

**\**Zostera marina* (Grass-wrack).** Flowers ? ♂, more probably unisexual and monœcious, the two sexes oc-

curing regularly intermixed in the same inflorescence in two longitudinal rows, one row on each side of the central vascular strand of the spadix. In each row ♂ and ♀ flowers occur alternately, one above the other, and those of the one sex in the one row stand nearly but not quite level with those of the other sex in the other row. On this view a ♂ flower consists of a single stamen similar to that of *Phyllospadix* (see above) subtended by a bract, the ♀ flower, which is bractless, of a single ovary as in *Phyllospadix* (see above) but without vascular bundles.

If the flower is regarded as ♀ it must be supposed to consist either of a stamen in the one row together with the ovary standing slightly above or below it in the other row; or, of a stamen together with the ovary above or below it in the same row. The former alternative appears to be negatived by the fact that stamen and ovary arise on opposite sides of the central vascular strand of the axis (spadix), the latter by the position of the bract accompanying the stamen which would, presumably, occur in the median plane beneath each flower were it in fact ♀; and also by the character and orientation of the anther-bearing structures which, presumably, represent tepal and stamen (see above under *Potamogeton*, *Ruppia* and *Phyllospadix*). Furthermore, it is to be noted that the lowest stamen in a row may sometimes be situated so nearly in the mid-line that the two halves of the anther straddle the axial vascular strand, no gynæceum being developed sufficiently near this level to be considered as a component of the same flower as this stamen. This arrangement is compatible with a unisexual construction, but improbable if the flower is normally ♀. Since the gynæceum is without differentiated vascular bundles it is uncertain here as in *Phyllospadix* whether four or two carpels are present or indeed, if four carpels are, in fact, present in *Phyllospadix*, whether only three are formed

in *Zostera* owing to the disappearance of the anterior member; and whether if this is so this loss is the cause of the formation of only a single horn-like prolongation of the ovary downwards below the ovule as compared with two prolongations in *Phyllospadix*, or whether this difference in the two genera is merely the result of different space and pressure relations.

## 175. NAIADACEÆ

Aquatic plants. Flowers unisexual, generally monœcious, rarely dicœcious, solitary or a few aggregated together, naked or enclosed in a spathe, with or without a perianth. ♂ Flower. A 1. Anther entire. ♀ Flower. G 2, 3 or 4, sterile + ? 1, fertile. Ovary syncarpous, unilocular. Ovule solitary, basal. Style short. Stigmas 2, both receptive; or 3, all receptive or modified in varying degree into spine-ended filaments which become wholly or partially non-receptive; or 4 in two pairs, one pair receptive the other spine-ended and non-receptive. Fruit one-seeded. Seed-coat adherent to the pericarp.

The number of carpels forming the wall of the ovary is indicated by the number of stigmas. Since when 2 or 3 in number the stigmas may be alike and when 4 are differentiated into two pairs, and since the ovule is invariably solitary and basal it seems probable that it is not borne by one of the stigma-bearing carpels. Analogy with other more highly differentiated types having a syncarpous unilocular ovary with a single basal ovule suggests that the tissue from which the ovule springs corresponds with a carpel of an inner whorl. The differentiation of the stigmas of some species into dissimilar pairs, one receptive and one not, finds a parallel in *Pæpalanthus* and its allies among Eriocaulaceæ (see later in the present Volume, Part 16, p. 558), but with the difference that in *Pæpalanthus* the dissimilarity in form is strictly associated with sterility and fertility of the two different kinds of carpels, whereas in *Naias* the two extreme forms are connected by a series of partially functional intermediate grades.

## ILLUSTRATIVE TYPES

**\**Naias flexilis*.** Flowers monœcious. ♂ Flower. Spathe and perianth present. ♀ Flower naked. Stigmas generally 4 in two pairs, sometimes 3, one of which is non-receptive.

**\**N. graminea*.** Flowers monœcious. ♂ and ♀ Flowers naked. Stigmas 2.



## 176. SCHEUZERIACEÆ (JUNCAGINACEÆ)

Marsh plants. Flowers generally ♂, rarely polygamous or diœcious, actinomorphic, hypogynous. Full floral ground-plan.  $T\ 3 + 3\ A\ 3 + 3\ G\ 3 + 3$ , apocarpous (12, p. 468†). Ovaries monocarpellary. Ovules solitary. Reduction from the full ground-plan frequent as illustrated below in the two hermaphrodite genera *Triglochin* and *Scheuzeria*.

*Triglochin maritimum*  $T\ 3 + 3\ A\ 3 + 3\ G\ 3 + 3$ , all fertile (1†, 12†).

*Scheuzeria palustris*  $T\ 3 + 3\ A\ 3 + 3\ G\ 3 + 3$ , 2 or 1, generally all fertile (12†).

*Triglochin palustre*  $T\ 3 + 3\ A\ 3 + 3\ G\ 3 + 3$  reduced, sterile (1†).

*T. Barrelieri*  $T\ 3 + 3\ A\ 3 + 3\ G\ 3 + 0$  (12, p. 470, Figs. 42, 43).

*T. montevidense*  $T\ 3 + 0\ A\ 3 + 0\ G\ 3 + 0$ .

### ILLUSTRATIVE TYPES

\**Triglochin maritimum* (1, p. 477, Fig. 57; 12, p. 470, Figs. 38–41). See above.

\**T. palustre* (Arrow-grass) (1, p. 477, Fig. 56). See above.

\**Scheuzeria palustris* (12, p. 470, Fig. 44). See above.

## 177. ALISMATACEÆ

Aquatic or marsh plants, with laticiferous tissue. Flowers generally ♂ sometimes unisexual (*e.g. Sagittaria*), hypogynous, actinomorphic.  $K\ 3\ C\ 3\ A\ 3_2 + 0$ , or 6 in a single whorl, or  $\infty\ G\ 3 + 3$  or  $\infty$ , apocarpous. Ovaries monocarpellary, with a single ovule, or rarely two or more.

## ILLUSTRATIVE TYPES

\****Alisma Plantago*** (Water Plantain) (12, p. 468, and Figs. 45-47). Receptacle flat.  $K\ 3\ C\ 3\ A\ 6\ G$  numerous (18-30) standing in one ring. Ovules solitary in each ovary. Style becoming sub-terminal as the ovule develops as in some apocarpous genera in other Families (*e.g. Xanthorrhiza* among Ranunculaceæ).

The six stamens stand in one ring on radii alternating with those of the perianth members. Their vascular bundles turn out from the central vascular cylinder independently on these same radii. These facts indicate a change of ground-plan from trimerous to hexamerous whorls following upon a process of reconstruction in the central vascular cylinder, the six stamens alternating with the calyx and corolla as though the whole perianth represented a single whorl. Another change of ground-plan occurs at the formation of the gynæceum, the numerous ovaries being arranged in one ring on a flat receptacle. Outer epidermis of the base of the ovary wall where the ovaries are in contact glandular.

\****Echinodorus (Alisma) ranunculoides***.  $K\ C$  and  $A$  as in *Alisma Plantago* (see above), but the carpels develop at different levels on a convex receptacle, hence the ovaries come to form a globular head.

\****Elisma (Alisma) natans***. Receptacle flat.  $K\ C\ A$  and  $G$  as in *Echinodorus ranunculoides* (see above).

\****Damasonium stellatum***. Receptacle flat.  $K\ 3\ C\ 3\ A\ 3_2\ G\ 3 + 3$ .

The vascular bundles for the six stamens do not arise directly from the central cylinder as in *Alisma*, but are carried out conjoined with two marginal veins of each sepal as in *Hydrocharis* (see under Hydrocharitaceæ later in the present Volume, Part 15, p. 543). The sepals are so broad that these

marginal veins lie far apart so that the staminal bundles detached from them, and therefore the stamens they serve, come to lie on the intermediate set of radii, thus giving the appearance of a hexamerous whorl alternating with the perianth as a whole (*i.e.* as though calyx and corolla constituted one whorl), and also with the six carpels (ovaries). For a similar duplication of the antesealous staminal whorl among Dicotyledons see under *Lawsonia* (Lythraceæ) earlier in the present Volume, Part 10, p. 275).

**\*Sagittaria sagittifolia** (Arrowhead) (12, pp. 468, 469, with Figs. 48-50). Flowers unisexual and monœcious in few-flowered whorls in the upper region of the stem, the upper whorls ♂, the lower ♀. ♂ Flower. K 3 C 3 A ∞. ♀ Flower. K 3 C 3 G ∞. Ovaries in successive tiers.

## 178. BUTOMACEÆ

Aquatic plants. Inflorescence umbellate, or flowers several together in a fascicle (*Hydrocleis*). Flower ♂, or by abortion unisexual, actinomorphic, hypogynous or syngonous at the base.  $K\ 3\ C\ 3\ A\ 3_2 + 3$  or  $\infty\ G\ 6$  standing in line with the perianth members, sterile + 6 on the alternate radii, fertile. Septal glands present in the mid-line of the fertile carpels. Ovary syncarpous and multilocular at the base, becoming almost at once pseudo-apocarpous through median radial splitting of the fertile carpels by extension of the septal glands to the surface. Ovules covering the walls of the loculi except in the mid-line of the sterile carpels (12, p. 474, Fig. 65). Dehiscence of the separate fruits occurs on the ventral face, *i.e.* in the mid-line of the fertile carpels.

## ILLUSTRATIVE TYPES

**\*Butomus umbellatus** (Flowering Rush) (12, pp. 472, 473, and Figs. 55–58). Inflorescence umbellate. Flower ♂.  $K\ 3\ C\ 3\ A\ 3_2 + 3\ G\ 6$ , sterile + 6, fertile. Flower syngonous at the base. Ovary syncarpous below becoming pseudo-apocarpous as it becomes free from the surrounding perianth-stamen tissue (see above).

Of the nine stamens two stand in front of each sepal and one in front of each petal. The vascular bundles for the antesepalous pairs are carried out as in *Hydrocharis* (see under Hydrocharitaceæ, later in the present Volume, Part 15, p. 543) and in *Damasonium* (see earlier in the present Volume under Alismataceæ, Part 15, p. 538) conjoined with two marginal veins of each sepal; those for the antepetalous whorl are conjoined with the petal midrib bundles.

**Hydrocleis nymphoides** (known also under the names **H. Commersoni** and **Limnocharis Humboldtii**) (12, pp. 473-476, and Figs 59-64). Flower ordinarily ♂, hypogynous.  $K\ 3\ C\ 3\ A\ \infty\ G$  (generally) 6, sterile + 6, fertile. In depauperated specimens loculi are present, but the fertile carpels bear no ovules, being so much reduced that their vascular systems have almost disappeared.

## 179. HYDROCHARITACEÆ

Aquatic plants. Inflorescence or individual flowers enclosed in a spathe of one, or two conjoined bracts. Flowers generally unisexual and dioecious with rudiments of the non-functional sex, or less often ♀ (*e.g. Blyxa spp.*) or unisexual under some conditions and ♂ under other conditions (*Elodea spp.*), syngonous, actinomorphic, exceptionally slightly zygomorphic (*e.g. Blyxa spp.*). Generally trimerous throughout with an andræcium of 1-4 whorls and a gynæceum of 3 sterile and 3 fertile, or of 6 sterile and 6 fertile, or of 9-15 sterile and 9-15 fertile carpels, or of 3 fertile carpels only (12†). Ovary syncarpous, unilocular throughout or shortly becoming so as the fertile carpels fail to reach the centre. Stigmas centred over the sterile carpels when these are present, in their absence over the fertile carpels, generally either deeply bifurcate or split in two almost to the base, rarely entire (*Vallisneria, Blyxa*). Ovules generally numerous, scattered over the whole surface of the incomplete partitions formed of the fertile carpels when these project into the loculus (*e.g. Hydrocharis, Stratiotes*); or when these members scarcely project, over the whole inner face of the ovary wall except over the sterile carpel midribs as in Butomaceae (see earlier in the present Volume, Part 15, p. 540). Fruit generally indehiscent.

## ILLUSTRATIVE TYPES

\***Hydrocharis Morsus-ranæ** (Frogbit) (12, pp. 476, 477 and Figs. 73-78). Flowers unisexual and dioecious.

♂ Flower. K 3 C 3 A 3 + 3 + 3 + 3, the innermost whorl generally staminodal. A gynæceal rudiment is often present in the centre consisting of three filaments without differentiated vascular elements but standing

over the free ends of three vascular bundles and corresponding to three aborted sterile carpels. Surrounding these aborted carpels and separating them from the andræcium a 6-lobed, non-vascular, glandular disc.

The two superposed stamens situated on each perianth radius when the full complement is present are served by a single trunk cord, hence the suppression of the inner of the two whorls on either set of radii will not affect the radial position of the succeeding whorl.

♀ Flower. K 3 C 3, each with a superposed vascular glandular structure A 3 + 0 or  $3_2 + 0$  G 6, sterile, standing in line with the perianth members + 6, fertile, on the alternate radii, projecting far into the loculus as incomplete partitions. Styles 6, centred over the sterile carpels. Stigmas 6, generally bilobed, sometimes trilobed.

The antepetalous glands have a feebly developed vascular system derived from the petal midribs. When the antesealous staminal whorl is duplicated the vascular bundles of each pair are detached from a pair of lateral veins instead of from the midrib of the sepal. The separate origin from two sepal laterals of the vascular bundles of two stamens representing a duplicated antesealous staminal member occurs also in *Damasonium* among Alismataceæ and in *Butomus* among Butomaceæ (see under these Families earlier in the present Volume, Part 15, pp. 538 and 540, respectively); and among Dicotyledons in *Lawsonia* among Lythraceæ (see earlier in the present Volume, Part 10, p. 275). As the loculus closes the fertile carpels undergo median radial splitting from within outwards. Each of the six styles receives three vascular bundles, a sterile carpel midrib and half the vascular system of the neighbouring fertile carpel on each side, and thus corresponds to  $\frac{1}{2} 1 \frac{1}{2}$  carpels. As a rule the sterile carpel midrib shortly comes to an end and the stigma is then bilobed, but occasionally it persists and the stigma then shows a third, middle lobe in line with the sterile carpel.

\***Elodea spp.** Flowers unisexual and diœcious or sometimes ♀ (see above under characters of the Family). ♂ Flower (e.g. *E. densa*). K 3 C 3 A 3 + 3 + 3, all with anthers and with filaments having undifferentiated vascular strands + 3 non-vascular filaments without

anthers  $\pm 3$  gynæceal rudiments. ♀ Flower (e.g. \**E. canadensis*, Canadian Water-weed, *E. crispa*). K 3 C 3  $\pm 3$  non-vascular staminodes G 3, semi-solid, fertile. Stigmas 3, sessile, split in two almost to the base, centred over the three fertile carpels ('commisural').

*Vallisneria spiralis* (12, pp. 477, 480, and Figs. 84-89). Flowers unisexual and diœcious. ♂ Flower, K 3 C 3 A 3, all without differentiated vascular bundles G 0. ♀ Flower. K 3 C 0 A 0 G 3, semi-solid, fertile. Stigmas 3, sessile entire, channelled on the inner (upper) surface through partial median radial splitting on the ventral face from within outwards. Each with two vascular bundles through division in two of the fertile carpel bundles in accord with the above-mentioned partial radial split.

The disappearance of an outer sterile carpel whorl in *Vallisneria* and *Elodea* with consequent reduction of the gynæceum to a single whorl of semi-solid fertile carpels is comparable with the processes which have occurred in *Gossypium* among Malvaceæ (see under that Family in Vol. I, Part 4, p. 110), in many *Begonia spp.* (see under Begoniaceæ earlier in the present Volume, Part 7, p. 261), and in *Datisca* (see under Datisceæ, Part 7, p. 259).

*Blyxa* (e.g. a form in cultivation passing under the name of *B. flava*) (12, p. 476 and Figs. 66-72). K 3 C 3 A 1 + 2 (by reduction from 3 + 3), all three being situated on one side of the flower on neighbouring perianth radii, G 3, sterile + 3, fertile, projecting into the loculus almost to the centre, the incomplete chambers antesepalous. Style single. Stigmas 3, centred over the sterile carpels.

The three staminal bundles present are conjoined at first with the midribs of the three adjacent perianth members (one sepal and two petals) upon which they are superposed, hence the presence or absence of any members of the andrœcium does not affect the position of the sterile carpel midribs nor (it follows) of the incomplete loculi. The above incomplete development of the andrœcium renders the flower zygomorphic. Herein *B. flava* differs from another ♀ species, *B. echinosperma*, in which the flower is actinomorphic and the three persisting stamens antesepalous.



## 180. PALMÆ

Inflorescence rarely terminal, generally a large, axillary, simple or richly branched spike or panicle enveloped in a spathe-like bract. Flowers rarely ♀, usually unisexual, frequently with aborted rudiments of the non-functional sex, commonly diœcious, less often monœcious, seldom polygamous, hypogynous, generally trimerous. ♂ Flower.  $K\ 3\ C\ 3\ A\ 3 + 3$  or  $3 + 3_2$  or sometimes  $\infty \pm$  a rudimentary gynœceum. ♀ Flower.  $K\ 3\ C\ 3 \pm$  as many staminodes as there are stamens in the ♂ flower  $G$  (generally) 3, sterile  $+ 3$ , fertile, less often 6, sterile  $+ 6$ , fertile, or 9-15, sterile  $+ 9-15$ , fertile, or 3, fertile  $+ 0$ . Ovary syncarpous when two whorls of carpels are present, apocarpous when only one whorl is developed; when syncarpous trilocular or unilocular according as the fertile carpels reach, or fall short of the centre. Style (when present) single, terminal. Stigmas as many as the sterile carpels and centred over these carpels. Ovules solitary in each loculus. Fruit drupaceous or baccate, generally one-seeded through early abortion of all the ovules but one.

## ILLUSTRATIVE TYPES

**Cocos nucifera** (Cocoa-nut Palm). Flowers monœcious. ♀ Flower.  $G\ 3$ , sterile  $+ 3$ , fertile. Ovary syncarpous, unilocular. Fruit drupaceous.

**Phœnix dactylifera** (Date Palm), **P. sylvestris**. Flowers diœcious. ♀ Flower.  $G\ 3$ , fertile  $+ 0$ . Ovary apocarpous. Fruit baccate.

The apocarpous character of the gynœceum is readily observed in ripe fruits as ordinarily obtained commercially to which the 'cup' formed by the persistent perianth is still attached. When the ripe date is gently removed

from this cup the two aborted ovaries (carpels) are exposed attached to the bottom of the cup.

**Chamærops humilis.** Flowers diœcious or polygamous.  $A\ 3 + 3$  or  $3_2 + 3$  through duplication of the members of the outer whorl.  $G\ 3$ , fertile + 0, apocarpous. Style very short, channelled on the inner face (as in many types when formed of a single carpel) the channel opening out in the region of the characteristically zygomorphic stigma which is papillose only on this face.

## 181. CYCLANTHACEÆ

Flowers unisexual, both sexes being distributed in a regular pattern over the whole surface of an unbranched club-shaped axis (spadix). ♂ Flower. Perianth absent or formed of a ring of numerous thick teeth.  $A\ 6-\infty$   $G\ 0$ . ♀ Flower syngonous. Perianth absent, or in the form of teeth crowning the ovary, or of four tepals. Staminodes 4, in types with tepals superposed upon them.  $G\ 4$ , sterile + 4, fertile or 2, sterile + 2 fertile. Gynæceum almost completely sunk in the tissue of the spadix. Ovary syncarpous, unilocular, but partially chambered through the protrusion inwards of the fertile carpels. Ovules  $\infty$ , in numerous rows on each placenta. Stigmas as many as the sterile carpels and centred over these carpels, sessile or borne on a short thick style. Fruit a syncarp derived from the whole inflorescence, consisting of the spadix covered with the berry-like fruits of the individual ♀ flowers, the ♂ flowers having fallen. Seeds in each berry numerous.

## ILLUSTRATIVE TYPES

**Carludovica palmata.** Flowers arranged in the pattern of four ♂ flowers round each ♀ flower, one above, one below and one on each side. ♂ Flower.  $T$  numerous  $A\ \infty$ . ♀ Flower.  $T\ 4$   $A\ 4$  long, filamentous, staminodal superposed on the tepals  $G\ 4$ , sterile, alternating with the tepals + 4, fertile in line with the tepals. Stigmas sessile in the form of four tufts of papillæ at the angles of the four-sided free summit of the ovary, *i.e.* at the outer edge of the four slits by which the loculi open to the surface.

The boundaries of the gynæceum within the tissue of the spadix are not defined in the ordinary way. Each occupies an 'island' area of tissue circumscribed by the horizontal strands of a vascular meshwork within which the placental

strands are the only bundles present at this level. Towards the surface of the spadix the meshwork gives rise to a broad four-sided ring of numerous bundles occupying the periphery of the 'island' areas. A bundle detached from the inner face of this ring on each tepal radius becomes the bundle of the superposed staminode. A bundle similarly detached on each alternate radius and standing at the outer angle of the closing loculus represents the midrib of a sterile carpel. The remaining bundles of the ring serve the tepals.

The flat summit of the ovary is marked off into four areas through median radial splitting of the fertile carpels, each area showing a median radial groove where the loculus opens to the surface.

## 182. ARACEÆ

Flowers ♂ or unisexual and then generally monœcious, disposed on a fleshy axis (spadix) in the form of a generally many-flowered, bractless spike accompanied by a large sheathing bract (spathe); varying from the full monocotyledon ♀ type  $T\ 3 + 3\ A\ 3 + 3\ G\ 3$ , sterile + 3, fertile, being then hypogynous, to naked unisexual flowers, sometimes reduced to the limit of  $A\ 1$  in the ♂ (e.g. *Arisarum*) and to  $G\ 1$ , sterile + 1, fertile in the ♀ (e.g. *Arum*, *Arisarum*, *Pistia*). Tepals free or united. In ♂ flowers the stamens generally more or less conjoined; sometimes completely, forming a synandrium. The number of filaments composing the single column of the synandrium may be indicated by the number of vascular bundles, but the fusion is sometimes so complete that the component bundles are 'condensed' into a single cord. Filaments when more or less separate often very short, passing into a broad connective in which the single vascular bundle proper to the filament may fork, the two branches diverging, one towards each theca (anther sac). In ♀ flowers staminodes present or absent. Gynæceum syncarpous. Ovary tri-, bi- or unilocular according as the fertile carpels extend to the centre or not. Style single, or stigma sessile and then generally dome-shaped. Ovules 1 to numerous in each loculus. Fruit baccate.

When the flowers lack a perianth and are densely crowded the limits of each individual are often not to be determined by inspection of the mature stage. It may then be necessary either to dissect a portion of the inflorescence or to observe it at an early stage of development.

## ILLUSTRATIVE TYPES

\***Acorus Calamus** (Sweet Flag). Flower ♂.  $T\ 3 + 3\ A\ 3 + 3\ G$  (generally) 3, sterile + 3, fertile, syncarpous.

Ovary trilocular. Ovules in several rows in each loculus. Stigma almost sessile.

The single central vascular cord which enters the base of the gynæceum consists of the three fused placental bundles of the three fertile carpels, both sterile and fertile carpels being without separate midrib bundles. Towards the top of the ovary these three bundles separate. Each divides in two. The resulting twin bundles of each pair diverge, each approaching the mid-line of the neighbouring sterile carpel on the corresponding side. These bundles serve the stigmas which are centred over the sterile carpels. Hence each stigma represents a sterile carpel flanked on each side by half a fertile carpel ( $\frac{1}{2} \times \frac{1}{2}$ ).

**Anthurium.** Flower ♂. T 2, lateral + 2, median A 2, lateral + 2, median G 2, lateral, non-vascular, sterile + 2, median (actually or potentially) fertile. Ovary four-angled and bilocular below, becoming unilocular above as the fertile carpels fail to reach the centre. Ovules 1 or 2 in each loculus. Stigma almost sessile, dome-shaped.

**\*Arum maculatum** (Cuckoo-pint, Lords and Ladies). Flowers unisexual, monœcious, in successive zones up the spadix in the order (1) ♀ functional, (2) ♀ barren, (3) ♂ functional, (4) ♂ barren. ♀ Functional. T o A o G 2, 1 sterile, 1 fertile. Ovary smooth-walled, rounded, unilocular. Ovules several, 2 or 3 abreast. Stigma sessile, dome-shaped, surmounting both carpels. ♀ Barren. T o A o G 1 sterile, angular from pressure, with outgrowths on the angles, + o, the fertile carpel with loculus and ovule being suppressed. Style long, filiform, non-receptive, terminating the sterile carpel. ♂ Functional. T o A 1-4, filaments very short G o. ♂ Barren. The stamens reduced to antherless staminodes, each prolonged above into a long hair-like filament. Spadix projecting considerably beyond the topmost zone of flowers.

In the different conformation of the ovary, style and stigma in the functional and barren ♀ flowers, respectively, comparison may be made with the dissimilarity between the gynæcea of the functional and barren ♀ flowers in the Bulrush

(*Typha*) (see earlier in the present Volume under Typhaceæ, Part 15, p. 523; also 12, p. 462, Figs. 1 and 2). But in *Typha*, in which, unlike *Arum*, the barren as well as the functional gynæcea are constructed of two carpels, it is in the fertile flower that the style is formed of a single sterile carpel and is long and filamentous, ending (since here the sterile member alone is receptive) in the broad flattened form of stigma so often characteristic of the single valve carpel. While it is in the barren flower with the two similar carpels contributing equally that the style is shortened to a mere central stump.

***Zantedeschia æthiopica*** (known also under the names ***Calla æthiopica*** and ***Richardia africana***) (*Arum* Lily). Flowers unisexual, monœcious. ♂ Flower. T o A 2 or 3 G o. ♀ Flower. T o A (generally) 3, staminodal G 1-5, sterile + 1-5, fertile. Ovary with as many loculi as fertile carpels at the base where these carpels extend to the centre, becoming unilocular above as they cease to reach the centre. Ovules in two rows in each loculus. Style short. Stigma dome-shaped.

***Spathicarpa sagittifolia***. Flowers unisexual, monœcious, in 4-5 rows on the spadix which is united throughout its length with the spathe. ♂ Flower. T o A a synandrium of (generally) 4 stamens (sometimes of 3 or 5), G o. ♀ Flower. T o A (generally) 4, separate, staminodal G 2, 1 sterile, 1 fertile. Ovary unilocular with one basal ovule. Style thick. Stigma dome-shaped.

***Pistia Stratiotes***. Flowers unisexual, monœcious; in each inflorescence one ♀ below, a few ♂ above. ♂ Flower. T o A a synandrium of 2 stamens G o. ♀ Flower. T o A o G 2, 1 sterile, 1 fertile. Ovary unilocular. Ovules in numerous rows. Below the ♂ flowers a flattened, membranous vascular outgrowth, possibly representing a zone of modified sterile flowers.

## 183. LEMNACEÆ

Flowers unisexual and monoëcious, in three-flowered inflorescences (2 ♂ 1 ♀) with spathe (*Lemna*, *Spirodela*), or in two-flowered inflorescences (1 ♂ 1 ♀) without a spathe (*Wolffia*). Perianth absent. ♂ Flower. T o A 1. ♀ Flower. T o G 2, syncarpous, 1 sterile, 1 fertile. Ovary unilocular, open to the exterior above through the short hollow style the rim of which has an even, unbroken outline. Ovules 1-6, basal.

## ILLUSTRATIVE TYPES

**\*Lemna** (Duckweed). Inflorescence three-flowered, 2 ♂, developing successively 1 ♀.

**\*L. minor** (Lesser Duckweed), **\*L. trisulca** (Ivy-leaved Duckweed). Ovule solitary.

**\*L. gibba** (Gibbous Duckweed). Ovules 4-6.

A vascular bundle passes into the filament of the stamen in the ♂ flower. In the ♀ flower the single vascular cord which supplies the gynæceum gives rise to the sterile carpel midrib which continues up into the style, and in *L. gibba* to a group of 4-6 strands which spring from a common nodal point and supply a corresponding number of ovules. The above vascular scheme, together with the actinomorphic form of the style apex, indicate that the gynæceum is bicarpellary and that the vascular system of the fertile carpel comes to an end at the level of origin of the ovule(s).



## Part 16

### Monocotyledons

Family	184.	Restionaceæ
„	185.	Eriocaulaceæ
„	186.	Bromeliaceæ
„	187.	Commelinaceæ
„	188.	Pontederiaceæ
„	189.	Dioscoreaceæ
„	190.	Burmanniaceæ



## 184. RESTIONACEÆ

Flowers almost always unisexual, often with rudiments of the non-functional sex, diœcious or less often monœcious, hypogynous, actinomorphic, generally trimerous, sometimes dimerous. Full ground-plan.  $T\ 3 + 3\ A\ 0 + 3\ G\ 3$ , sterile, superposed on the outer perianth members + 3 (actually or potentially), fertile, on the radii of the inner perianth members. Or similarly dimerous throughout. ♂ Flower with a rudimentary gynœceum. ♀ Flower. Stamens replaced by staminodes or lacking. Ovary tri- or bilocular, or unilocular, according as the fertile carpels extend to the centre or not. Ovules solitary in the loculi, pendulous, sometimes only one loculus fertile. Styles distinct, as many as the sterile carpels and centred over these carpels, or connate for a longer or shorter distance; stigmatic only at the top, or papillose or feathery almost throughout their length. Fruit a capsule splitting in line with the loculi, or nut-like and indehiscent.

Although the members of the outer staminal whorl no longer attain recognisable form and their vascular bundles have been entirely lost they are probably still represented, at least in some genera, by a ridge of non-vascular tissue which projects in the mid-line from the inner face of the base of each outer perianth segment and is continuous with the tissue of the inner perianth segment on each side at the level at which these segments are about to separate. The persistence of this tissue remnant of the antesepalous stamen whorl would serve to explain how it comes about that the surviving whorl of functional stamens in the ♂ flower and that of the corresponding staminodes in the ♀ flower, having vascular bundles which turn out independently from the central cylinder, are nevertheless developed on the petal radii. The antesepalous stamen bundles when not yet lost must also, no doubt, have arisen independently from the central cylinder since the existing scheme would not otherwise be in accord with normal regular alternation in the vascular ground-plan. That in these circumstances the outer, sterile carpels (and hence the loculi) should be situated on the sepal radii may

be accounted for by the fact that the ovary has already become disjoined from the tissue of the outer whorls at the level at which the bundles for these carpels turn outwards from the central cylinder. For were these structures still conjoined the expectation would be that owing to the existence of that state of 'congestion' which is visualised as becoming set up in six-whorled types in which the vascular bundles for all the whorls originate independently the development of these carpels (and hence of the loculi) would take place on the petal radii (see Vol. I, Introduction, p. 8). In another isomerous six-whorled Monocotyledon type, similarly exceptional in that the vascular bundles for the two staminal whorls turn out from the central cylinder independently, the development of a distinct stipe to the ovary has the same effect of permitting the regular alternation of all the whorls (see later in the present Volume under *Zebrina* among Commelinaceæ, Part 16, p. 562). Fertile carpels with placental but without midrib bundles. Only the sterile carpel bundles are prolonged into the style(s).

### ILLUSTRATIVE TYPES

**Restio.** See the characters of the Family.

## 185. ERIOCAULACEÆ

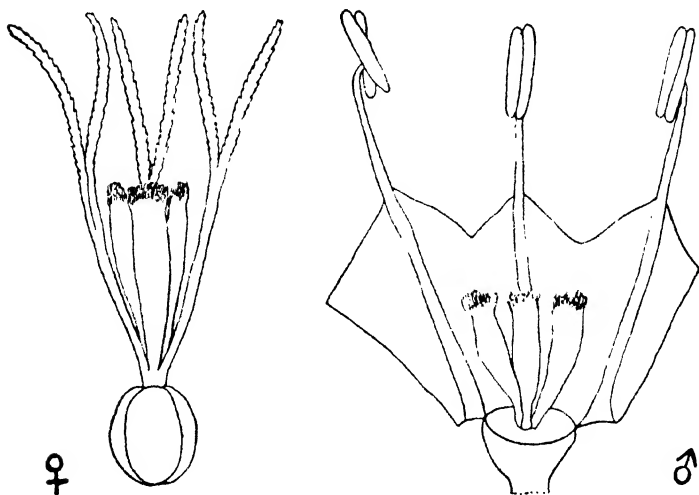
Inflorescence generally a dense capitulum surrounded by bracts and borne on a leafless peduncle. Flowers unisexual by abortion, both sexes occurring together in the capitula, but not strictly or uniformly arranged, the ♂ being mostly to the outside in some species, the ♀ in others, but always with some intermixing of the two forms. Both ♂ and ♀ flowers with rudiments of the non-functional sex. Flowers of both sexes generally trimerous throughout, less often dimerous. Perianth two-whorled, rarely one-whorled through suppression of the inner whorl. Inner whorl actinomorphic or zygomorphic. Androecium two-whorled, or one-whorled through suppression of the outer whorl. Gynæceum two-whorled, the outer carpels antesealous and sterile, the inner antepetalous and fertile. Ovary syncarpous, tri- or bilocular according as the fertile carpels, which reach to the centre, are three or two in number. Style single, dividing above into as many arms as there are sterile carpels, the arms standing over these carpels; or styles distinct and standing over both sterile and fertile carpels, those of the sterile carpels then functionless, those of the fertile carpels ('commissural') generally of different form and alone receptive (3, pp. 157, 158†). Fruit a capsule, dehiscing loculicidally.

## ILLUSTRATIVE TYPES

\***Eriocaulon septangulare** (Pipewort). Flowers dimerous. ♂ Flower.  $K\ 2\ C\ 2\ A$  (when fully developed)  $2 + 2\ G\ 2$  (pistillodes) + o. ♀ Flower.  $K\ 2\ C\ 2\ A\ 2 + 2$ , both whorls in the form of very small non-vascular staminodes,  $G\ 2$ , sterile, antesealous + 2, fertile, antepetalous. Style single, with arms corresponding in number

with the sterile carpels, standing over these members, and bearing functional stigmas.

**Pæpalanthus** (Fig. 38), a 'key' genus. Flowers trimerous or dimerous. ♂ Flower.  $K\ 3\ C\ 3\ A\ 0 + 3\ G\ 3$  (pistillodes), antesepalous, sterile, bearing functionless stigmas + 0. Or with a corresponding number of dimerous whorls. ♀ Flower.  $K\ 3\ C\ 3\ A\ 0 + 3$  reduced



*Pæpalanthus* (*Platycaulon*) *vellozioides*. Gynoecium of ♀ flower (left). Inner perianth (split open), androecium and outer carpel whorl of the ♂ flower (right).

FIGURE 38.

to minute non-vascular staminodes  $G\ 3$ , antesepalous, sterile with styles bearing functionless stigmas + 3 antepetalous, fertile, with simple or forked styles bearing functional stigmas ('commissural'). Or with a corresponding number of dimerous whorls. In most species (e.g. *P. vellozioides*) the two sets of stigmas in the ♀ flower are of different form, those of the outer sterile whorl (not of the inner whorl, as incorrectly described previously)

being similar to the one set present in the ♂ flower. Here, as in various other diœcious genera (see under Rutaceæ) in Vol. I, Part 3, p. 85, and under Hydrocharitaceæ earlier in the present Volume, Part 15, p. 543), infertility in the ♂ flower is due to suppression of the inner carpel whorl.

The ♀ flower of *Pæpalanthus* (and other allied genera) furnishes an example of the rare condition, obtaining also in *Aphyllanthes* (Liliaceæ) and in the section *Ureneæ* of the Malvaceæ (see under these Families in Vol. I, Part 2, p. 65, and Part 3, pp. 107, 108, respectively); and in *Tripetaleia* (Ericaceæ) and *Ecballium* (Cucurbitaceæ) (see under these Families earlier in the present Volume, Part 11, p. 397 and Part 14, p. 495, respectively) in which all the carpels of a syncarpous gynœceum, both fertile and sterile, bear distinct styles or stigmas.

The above mentioned external features of the ♂ and ♀ flowers of *Pæpalanthus* and allied genera (unfortunately not generally procurable) render these types admirable material for demonstrating carpel polymorphism since only through recognition of the presence of two whorls of dissimilar carpels does it become possible to account for the different forms of the gynœceum in the two sexes.

## 186. BROMELIACEÆ

Flower almost always ♂, actinomorphic and trimerous, six-whorled (K 3 C 3 A 3 + 3 G 3, sterile + 3, fertile), hypogynous or more or less syngynous. Ovary trilocular, sometimes becoming unilocular above as the fertile carpels fail to reach the centre. Ovules in two or several rows in each loculus. Style single. Stigmas 3, centred over the sterile carpels. Fruit a berry, usually crowned by the persistent calyx, or a capsule; exceptionally compound, being derived from the whole many-flowered inflorescence (*Ananassa sativa*, Pineapple).

## ILLUSTRATIVE TYPES

**Bilbergia spp.** Flower syngynous. Ovules in two rows in each loculus. Fruit a dry berry.

**Pitcairnia.** Flower partially syngynous. Ovules in several rows in each loculus. Fruit a capsule dehiscing septically through median radial splitting of the fertile carpels.

The axial central cylinder enlarges at the flower base and becomes organised into a ring of six cords. The three standing in line with the sepals yield successively and centripetally the sepal midribs, antesealous stamen bundles and sterile carpel midribs; those in line with the petals similarly furnish sepal commissural marginal veins, petal midribs, antepetalous stamen bundles and the twin groups of placental strands of the fertile carpels, these carpels being without separate midrib bundles. Since neither the stamen nor the carpel bundles originate independently, the sterile carpels (and hence the loculi) are antesealous and the andræcium diplostemonous, notwithstanding that the flower is six-whorled and isomerous throughout (see Vol. I, Introduction, p. 8).

As the ovary becomes free from the outer whorls the fertile carpels become split in the median plane from without inwards. This split extends until it becomes continuous with the lumen of the septal gland and then with the stylar canal, thus leading finally to the separation of the three stigmatic arms, each representing a sterile carpel flanked on each side by half the neighbouring fertile carpel ( $\frac{1}{2}$  I  $\frac{1}{2}$ ).

**Tillandsia.** Flower hypogynous. Ovules in several rows in each loculus. Fruit as in *Pitcairnia* (see above).



# 187. COMMELINACEÆ

Flower ♂, actinomorphic or slightly zygomorphic through difference in form or inequality in size of the stamens, hypogynous, six-whorled, diplostemonous (see Vol. I, Part 2, p. 62, paragraph 2 ; 23, p. 657 ; 28, pp. 297, 298, 309-311†) ; very rarely five-whorled through loss of the antesealous stamen whorl (*Callisia spp.*) ; generally trimerous throughout (K 3 C 3 A 3 + 3 G 3, sterile + 3, fertile). Perianth whorls dissimilar, thus differing from those of Liliaceæ. Some stamens in one or both whorls often staminodal. Ovary syncarpous, trilocular through fusion of the fertile carpels in the centre, or sometimes bilocular through the closure of one loculus in which no ovules are developed. Style single. Stigmas 3, centred over the sterile carpels. Fruit a capsule, generally dehiscent, loculicidally through median radial splitting of the sterile carpels, seldom indehiscent.

As in other hypogynous six-whorled isomerous Monocotyledons, the diplostemonous andrœcium is associated with antesealous sterile carpels and loculi. The vascular bundles for the stamens turn outwards, at least in some genera (*e.g. Tradescantia, Commelina, Zebrina*, see 28, pp. 309-311 and Figs. 8-12), independently of the perianth midrib bundles, though it is not out of the question that they may in some types be derived from the same delimited central tract of vascular elements as these latter bundles. (Difficulty in determining this point arises from the fact that the central vascular tissue from which the bundles for the successive whorls are derived forms a plexus or solid core and that anastomosis sometimes takes place between the outgoing strands.) The avoidance of that state of 'congestion' regarded as leading in most hypogynous isomerous six-whorled Dicotyledons to antepetalous sterile carpels and loculi accompanied by obdiplostemony is, however, ensured in some genera (*e.g. Zebrina*), whether perianth and stamen bundles originate from a common tract or not, by the raising of the expanded region of the ovary upon a short free stipe (28, p. 310, Fig. 12 ; see also Vol. I, Introduction, p. 8, and under Caryophyllaceæ, Vol. I, Part 4, pp. 101, 102).

## ILLUSTRATIVE TYPES

**Tradescantia virginica** (Spiderwort). Flower actinomorphic.  $K\ 3\ C\ 3\ A\ 3 + 3$ , all similar and fertile  $G\ 3$ , sterile, antesepalous + 3 fertile, antepetalous.

**Commelina cœlestis**. Flower zygomorphic.  $K\ 3\ C\ 3\ A\ 3$  (2 fertile, 1 sterile) + 3 (1 fertile, 2 sterile); the three fertile stamens lie on adjacent radii on one side of the flower, the three staminodes on adjacent radii on the opposite side,  $G\ 3$ , sterile, antesepalous + 3, fertile, antepetalous.

**Zebrina pendula** (28, p. 309, Figs. 8-12). [N.B.—In Figs. 8, 9 the explanatory lettering is incorrectly rendered. For  $sm + st$  read simply  $sm$  and similarly for  $pm + st$  read  $pm$ . The antesepalous stamen bundles are superposed upon the sepal midrib bundles but are not carried out conjoined with them. They are seen in the Figure turning outwards from the centre in line with the sepal midrib bundles but distinct from them. The antepetalous stamens are similarly organised in the centre on the petal radii, but at the stage represented are not yet distinguishable.] Flower actinomorphic.  $K\ 3\ C\ 3\ A\ 3 + 3$ , all similar and fertile  $G\ 3$ , sterile, antesepalous + 3, fertile, antepetalous. Expanded region of the ovary raised on a short stipe. (For the connection between this development and the orientation of the carpels see above under the account of the Family.)

## 188. PONTEDERIACEÆ

Flower ♂, hypogynous, generally zygomorphic, trimerous throughout and six-whorled (K 3 C 3 A 3 + 3 G 3, antesepalous, sterile + 3, antepetalous actually or potentially fertile, sometimes five-whorled through suppression of the outer stamen whorl. Stamens springing from the perianth tube at various levels. Ovary trilocular, the fertile carpels extending to the centre. Style single. Stigma terminal, entire or slightly trilobed with the lobes standing in line with the sterile carpels. Ovules in two rows in each loculus, or single when two of the loculi remain empty. Fruit always enclosed in the persistent perianth, sometimes a many-seeded capsule, sometimes one-seeded and indehiscent.

The vascular bundles for the stamens do not arise independently but are conjoined at first with the perianth midrib bundles, becoming free later. Hence the suppression of the antesepalous whorl will not affect the radial position of the succeeding whorl. Sterile carpels with, fertile carpels without, separate midrib bundles. Only the sterile carpel midrib bundles are prolonged into the style, the placental bundles of the fertile carpels being used up in providing the strands to the ovules.

## ILLUSTRATIVE TYPES

**Elchhornia.** K 3 C 3 A 3 + 3 G 3, sterile + 3, fertile. Ovules in two rows in each loculus. Fruit a many-seeded capsule, dehiscing loculicidally through median radial splitting of the sterile carpels.

**Pontederia.** K 3 C 3 A 3 + 3 G 3, sterile + 3, of which only one is usually fertile. Ovary excentric. Ovule single. Fruit one-seeded, indehiscent.

The venation system of the perianth is exceptional in that the marginal veins of all six members are derived from six bundles lying on the intermediate set of radii which fork as they pass up the perianth tube, one branch of the fork entering

a sepal, the other a petal. Owing probably to the asymmetrical development and position of the gynæceum these six bundles arise irregularly, some originating independently from the central vascular complex, others arising with, but shortly becoming detached laterally from, an out-turning perianth-stamen bundle.

Although only one of the three potentially fertile carpels ordinarily bears an ovule, all three possess a similar vascular system consisting of twin placental strands.

## 189. DIOSCOREACEÆ

Flowers generally unisexual and dioecious with rudiments of the non-functional sex, rarely monoecious or ♂, actinomorphic, syngonous, isomerous throughout (K 3 C 3 A 3 + 3 sometimes staminodal G 3, antesepalous, sterile + 3, antepetalous, fertile). Ovary syncarpous, trilocular or very rarely unilocular through the fertile carpels becoming withdrawn from the centre at the base. Styles 3, cohering at the base, separating above into three simple or forked stigmas, centred in line with the sterile carpels. Ovules generally 2 in each loculus. Fruit a capsule or a berry.

## ILLUSTRATIVE TYPES

**\**Tamus communis*** (Black Bryony). Flowers dioecious. ♂ Flower. K 3 C 3 A 3 + 3 G 3, antesepalous, rudimentary + 0. ♀ Flower. K 3 C 3 A 3 + 3, both whorls staminodal G 3, antesepalous, sterile + 3, antepetalous, fertile. Ovary trilocular. Fruit a berry.

The vascular ground-plan at the flower base consists of six equidistant trunk cords. Those on the sepal radii break up into a sepal midrib, an antesepalous stamen bundle and a sterile carpel midrib; those on the petal radii similarly furnish a petal midrib, antepetalous stamen bundle and in a ♀ flower the placental bundle of a fertile carpel, these carpels being without a separate midrib bundle. As the loculi close the placental bundles, if they persist, divide in two and an interstitial slit (lumen of a septal gland) makes its appearance between the twin resulting strands. This slit extends outwards to the exterior and inwards to the stylar canal, thus defining the three styles each representing  $\frac{1}{2} + \frac{1}{2}$  carpels. In the ♂ flower no fertile carpels take shape and no placental bundle is detached from the antepetalous trunk cords. When the septal glands make their appearance the structures they separate represent the rudiments of sterile carpels which are reduced to three filamentous structures

**Dioscorea.** Fruit a capsule.

## 190. BURMANNIACEÆ

Flower ♀, generally actinomorphic rarely zygomorphic, more or less syngonous, six-whorled, or five-whorled through loss of the antesealous stamen whorl.  $K\ 3\ C\ 3\ A\ 3 + 3\ \text{or}\ 0 + 3\ G\ 3$ , antesealous, sterile + 3, antepetalous, fertile. Ovary trilocular or unilocular according as the fertile carpels extend to the centre or not. Ovules generally in several rows, sometimes only in two rows on each placenta. Style single. Stigmas 3, centred over the sterile carpels. Fruit a capsule sometimes opening at the top, or tearing between the carpel midribs, seldom separating into valves.

The vascular system below the flower generally consists of three cords. The middle portion of each of these cords turns outwards on a sepal radius. The two residual portions of each cord diverge, one portion fusing with the adjacent portion of the neighbouring cord on each side to form a cord on each petal radius. Hence at the flower base the whole system consists of a single cord on each perianth radius. The three cords on the sepal radii furnish the sepal midribs, the bundles for the antesealous whorl of stamens when these members are present and the sterile carpel midribs. The three on the petal radii similarly give rise to the petal midribs, antepetalous stamen bundles and the placental bundles of the fertile carpels, these carpels being without separate midrib bundles.

Above the ovule level the projecting placenta now non-vascular, the placental bundles having been used up in supplying strands to the ovules, show a median radial interstitial slit—the lumen of a septal gland.

The sterile carpel midribs are prolonged into the style which ends in three stigmatic arms formed through median radial splitting of the fertile carpels, each arm representing  $\frac{1}{2}$  or  $\frac{1}{3}$  carpels.

Since the vascular bundles of the stamens do not arise independently the loss in some types of the antesealous stamen whorl does not affect the radial position of the succeeding whorl.

## ILLUSTRATIVE TYPES

***Thismia hyalina*.** Flower actinomorphic.  $K\ 3\ C\ 3\ A\ 3 + 3\ G\ 3 + 3$ . Ovary unilocular.

**Gymnosiphon (Cymbocarpa).** Flower actinomorphic. K 3 C 3 A 0 + 3 G 3 + 3. Ovary unilocular.

**Burmannia.** Flower actinomorphic. K 3, with commissural marginal veins C 3 A 0 + 3 G 3 + 3. Ovary trilocular. The origin of each stigma from  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels is indicated in the outward form as well as being clearly evident in serial transverse sections of the style.

At the summit of the ovary anastomosing horizontal branches from the six primary vascular cords form a complete girdle, such as occurs in syngonous types in some other Families (*e.g.* Melastomataceæ, see earlier in the present Volume, Part 8, p. 288).





## ADDITIONAL ILLUSTRATIONS

relating to Families treated in Vol. I

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The Figures which follow illustrate the floral construction in various types included in nine Families treated in Vol. I, viz., Nymphæaceæ, Berberidaceæ, Papaveraceæ, Cruciferæ, Resedaceæ, Liliaceæ, Geraniaceæ, Linaceæ, Caryophyllaceæ. Some of these Figures (Figs. 39-42) have been introduced in order to illustrate types described but not figured in the accounts to which reference is made in the literature cited on pp. 135-137 in the present Volume (pp. 23-25 in Vol. I). The remainder (Figs. 43-48), reproduced from Diagrams which have already appeared in these accounts, serve to illustrate the modifications required in the Floral Diagrams in current use in order to exhibit the underlying relations of the vascular ground-plan to the floral ground-plan.

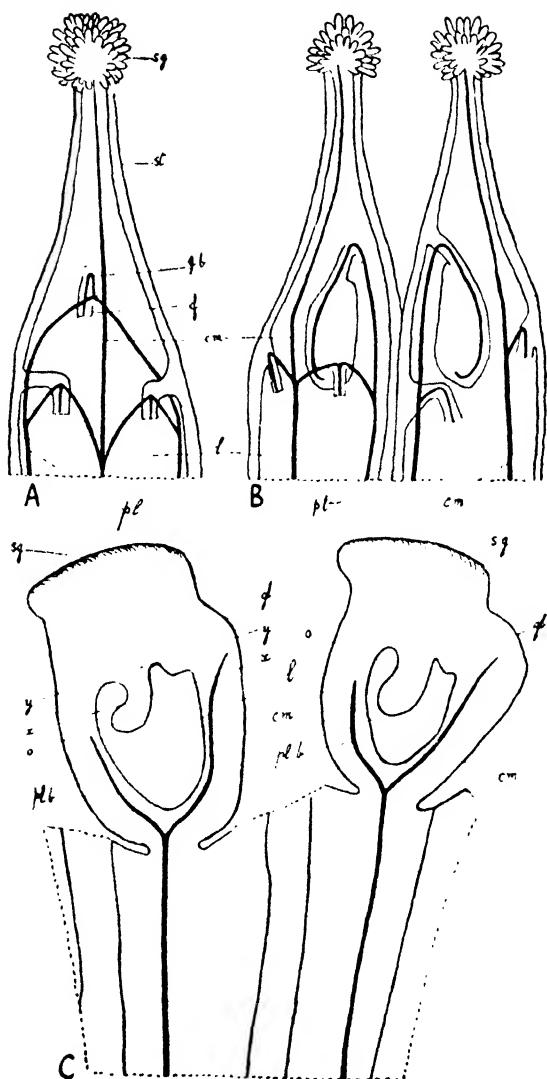


FIGURE 39.

FIG. 39. Nymphaeaceæ.

A, B. *Cabomba aquatica*. A. The upper region of a single ovary with style and terminal papillose stigma viewed as a transparent object from the ventral face, showing typical modes of suspension of the ovules; the two lower hang from the junction points of a lateral from the midrib bundle with a branch from one of the primary (placental) laterals; the single upper one from the junction point of the two primary (placental) laterals which come to an end at this level. B. The same region of two ovaries not yet completely separate viewed from the side. In the one (left) the upper ovule is suspended directly from one of the primary laterals. In the other (right) the upper ovule is similarly suspended; the lower on the left hangs from a branch of the primary lateral on that side which is not connected with the midrib bundle. [In order to expose the full vascular scheme the body of all the ovules in A and of all the lower ones in B has been cut away from the funicle.]

C. *Nelumbium speciosum*. Two young ovaries together with a portion of the peduncle in longitudinal section. [The tissue of the enlarged apex of the peduncle in which the ovaries are sunk has been cut away.] Each ovary shows the midrib bundle ending beneath a glandular protuberance and a placental strand derived from it not yet extending to the level of origin of the ovule. (For a fuller description see Vol. I, Part 2, pp. 29-31; also 29, pp. 217-220.)

*c m* carpel midrib, *f* funicle, *fb* funicle bundle, *gl* gland, *l* loculus, *o* ovule, *pl* primary lateral, *plb* placental bundle, *sg* stigma, *st* style, *x, y* the level of section represented in Fig. 40a and 40b, respectively.

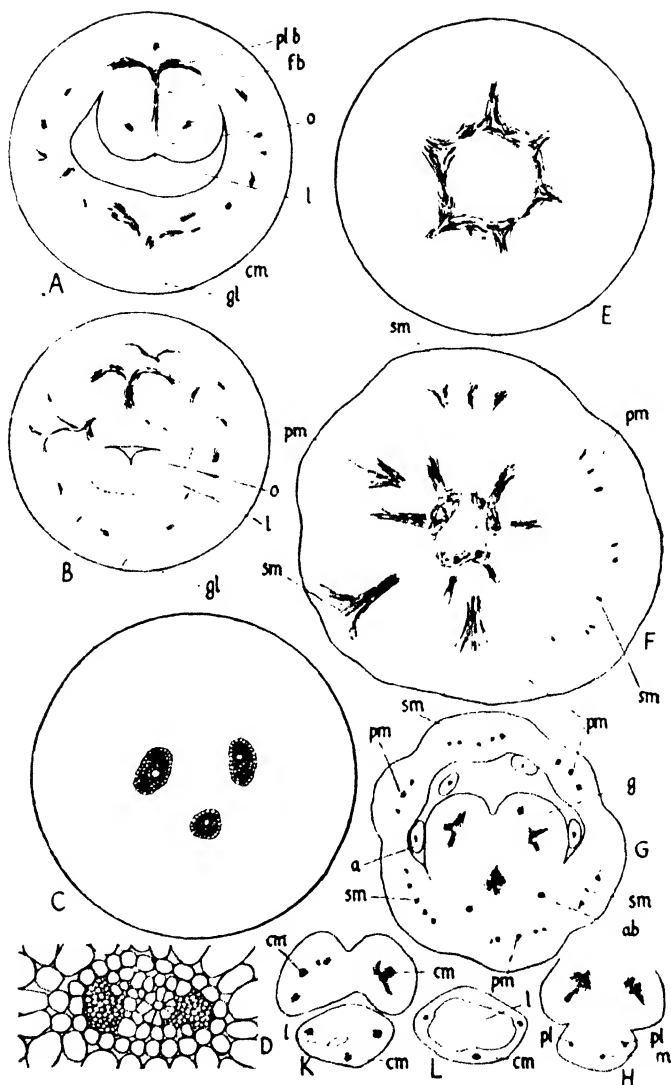


FIGURE 40.

FIG. 40. Nymphaeaceæ (continued).

A, B. *Nelumbium speciosum*. A. Transverse section of the ovary at the level (x in Fig. 39) at which the funicle bundle is given off from the placental bundles. B. The same at the level (y in Fig. 39) at which the loculus is almost closed. (For fuller details see 29, p. 220.)

C-L. *Cabomba aquatica*. C. Transverse section of the peduncle immediately below the flower. D. One of the two-bundled cords (steles) seen in C with some of the surrounding parenchyma more highly magnified. E. Transverse section of the flower base showing the vascular complex which precedes the formation of the bundles for the perianth. F. The same at the level at which the midrib bundles for the 3 sepals and the 3 petals have already left the central cylinder and those for the 6 stamens are in process of turning outwards. G. The flower cut slightly obliquely showing the perianth tube partially disjoined from the gynæceum, 4 of the 6 stamens already exerted, and the gynæceum of 3 ovaries not yet separate from one another, each with its vascular system which is becoming organised into a midrib and a pair of primary laterals. H, K. The gynæceum in transverse section showing stages in development and separation of the 3 ovaries and the development of their vascular systems. L. A single ovary in transverse section now separate and with the loculus fully formed. (For further details see references in the legend to Fig. 39.)

a stamen, a b stamen bundle, c m carpel midrib, f b funicle bundle, g gynæceum, gl gland, l loculus, o ovule, p l primary laterals, pl b placental bundle, p m petal midrib, s m sepal midrib.

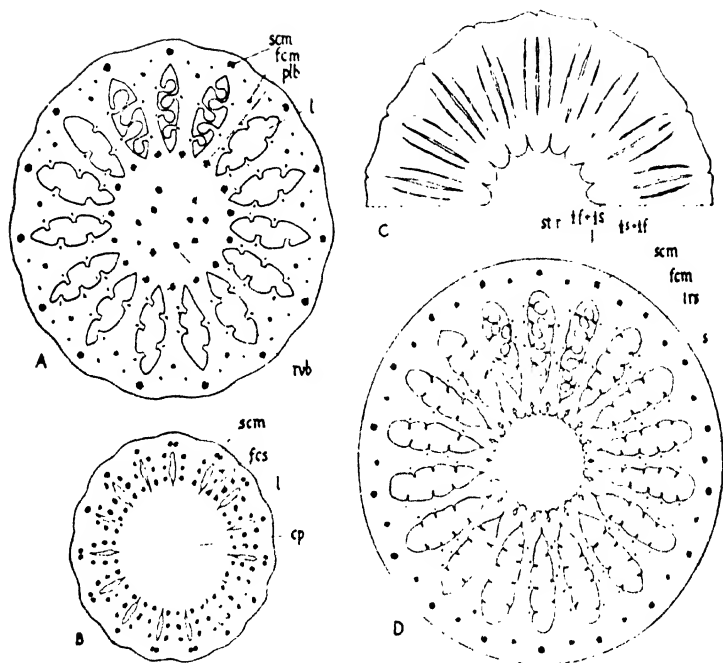


FIGURE 41.

FIG. 41. Nymphaeaceæ (continued).

A-C. *Nuphar luteum* (Yellow Water Lily). A. Transverse section of the ovary base after the appearance of the loculi and the organisation of the carpel midrib and placental bundles. In the centre residual vascular bundles of the axis. B. Transverse section at the level at which the ovary is about to pass into the short style. Many of the sterile carpel midrib bundles have divided in two. The fertile carpel vascular system is represented by a double row of strands in each septum. The centre is occupied entirely by parenchyma, the axial vascular strands seen in B having come to an end. C. Transverse section through half the stigmatic plate. In each stigmatic ray two vascular bundles. Each of these bundles represents half a sterile carpel midrib which has picked up in its course inwards half the system of the neighbouring fertile carpel on that side, the whole system of each ray may therefore be represented in terms of the corresponding carpels as  $\frac{1}{2}f + \frac{1}{2}s$ , the bracketed numbers indicating the split midrib of the sterile carpel, the unbracketed numbers half the system of the two neighbouring fertile carpels.

D. *Nymphaea alba* (White Water Lily). Transverse section from near the top of the ovary showing the initial radial splitting of the fertile carpels (septa) on their (at this level) free inner face which leads to the separation of the stigmatic rays which stand as in *Nuphar*, over the loculi. [For simplicity ovules have only been represented in three loculi in A and D.] (For further details see references in the legend to Fig. 39.)

*c p* central parenchyma, *f c m* fertile carpel midrib, *f c s* fertile carpel vascular system, *i r s* initial radial split, *l* loculus, *pl b* placental bundle, *r v b* residual vascular bundle, *s* space, *s c m* sterile carpel midrib, *st r* stigmatic ray,  $\frac{1}{2}f + \frac{1}{2}s$  one of the two bundles serving a stigmatic ray consisting of half a sterile carpel midrib combined with half the vascular system of a neighbouring fertile carpel.

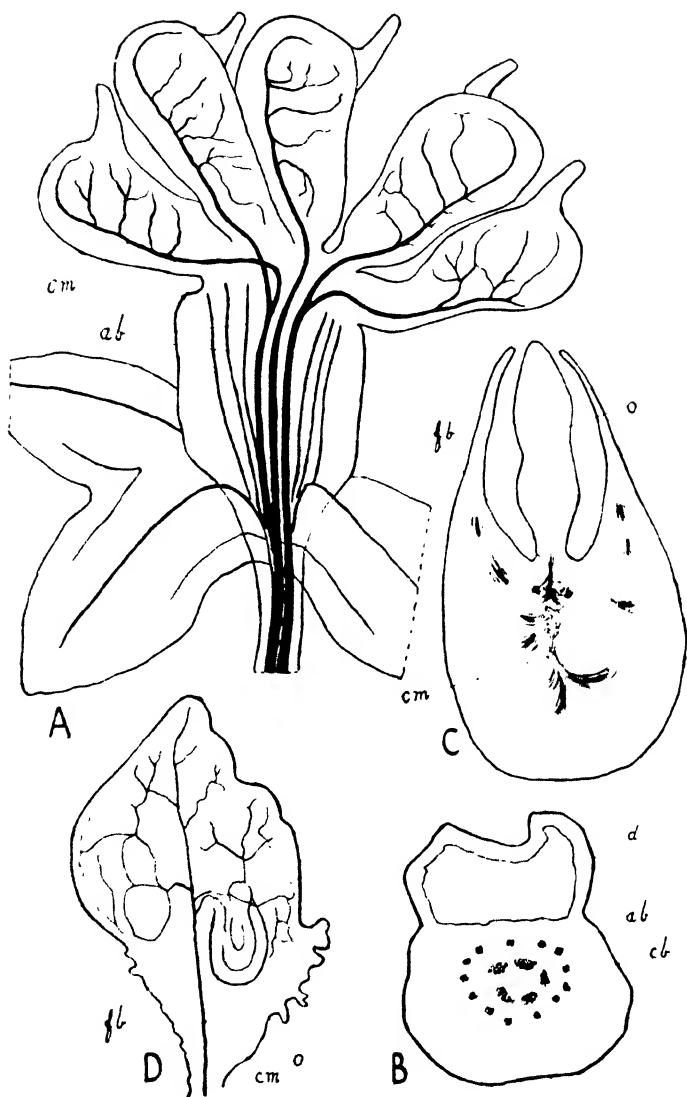
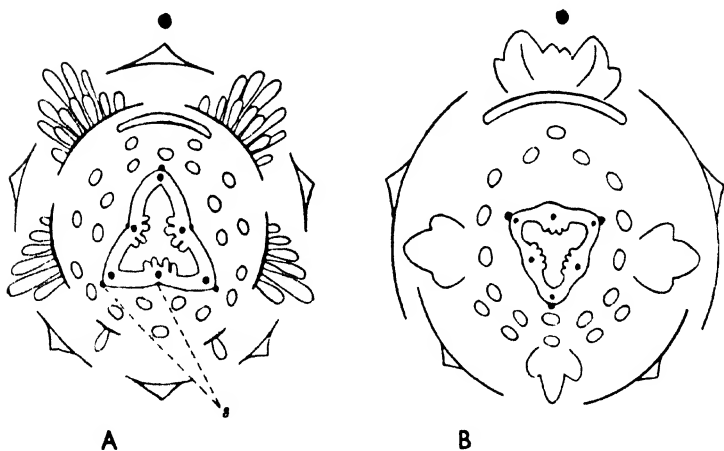


FIGURE 42.



FIG. 42. Resedaceæ. *Astrocarpus sesamoides*. A 'key' genus. A. Flower from which part of the calyx, and the petals and stamens have been cut away viewed as a semi-transparent object. Above, the apocarpous gynæceum of 5 monocarpellary ovaries, each ovary with a well-developed vascular system consisting of a midrib and numerous lateral branches. B. Transverse section of the middle (internodal) region of the flower between the level of exsertion of the perianth and the stamens. In the centre the ring of vascular bundles for the stamens and within this ring the five bundles for the five ovaries. At the back a large scale (disc). C. Transverse section of an ovary showing the origin of the funicle strand from the midrib, the large solitary ovule being seated on the midrib of the carpel which is of the semi-solid type. The ovary is open along the ventral suture. D. An ovary laid open along the ventral suture showing the origin of the funicle strand from the midrib in surface view. (D after Strasburger.)

a b stamen bundle, c b carpel bundle, c m carpel midrib, d disc, f b funicle bundle, o ovule.



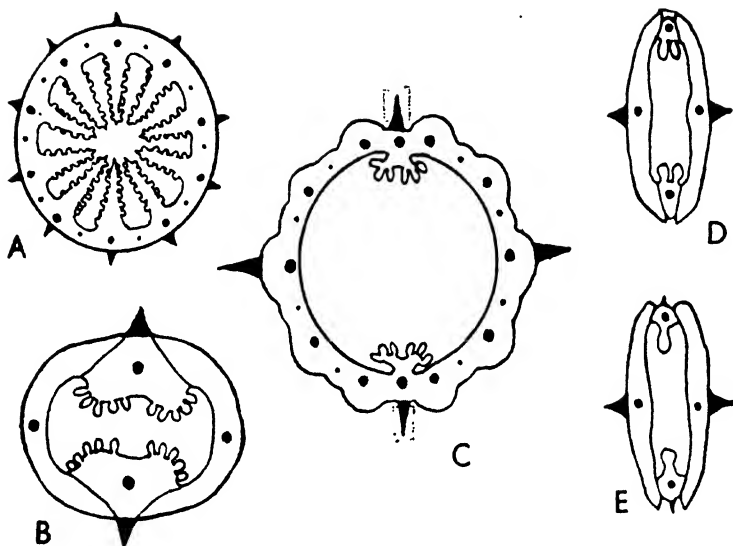
Resedaceæ (continued) (16, p. 110, Diagrams 15 (A) and 16 (B) reproduced).

A. *Reseda odorata*. G 6, 3 sterile + 3 fertile. Posterior median carpel sterile. Stigmas 6, 3 larger borne by the sterile carpels, 3 smaller by the fertile carpels ('commisural').

B. *Reseda luteola*. G 6, 3 sterile, 3 fertile. Posterior median carpel fertile. Stigmas 3, borne by the sterile carpels.

s stigmas.

FIGURE 43.



Papaveraceae. (Diagrams reproduced from 13, pp. 53 and 54.)

A. *Papaver* (Poppy). G 20, 10 sterile + 10 fertile. Stigmas 'commissural'.

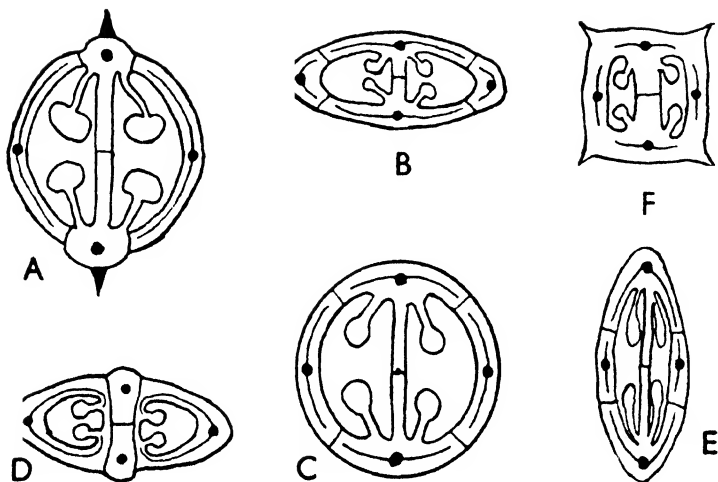
B. *Glaucium flavum*. G 4, 2 median, solid, fertile, 2 lateral, valve, sterile. Stigmas 'commissural'.

C. *Eschscholzia californica*. G 20, 8 valve, sterile 12 solid = 2 median, fertile, 10 sterile. Stigmas 4, 2 median ('commissural'), absent towards the end of the season, 2 lateral, always present.

D. *Corydalis cava*. G 4, 2 median, solid, fertile, 2 lateral, valve, sterile. Stigmas 2 lateral.

E. *Corydalis lutea*. G 4 as in D. Stigmas 4, 2 median ('commissural'), small, 2 lateral.

FIGURE 44.



Cruciferae. (Diagrams reproduced from 13, p. 54.)

A. *Cheiranthus Cheiri* (Wallflower). G 4, 2 median, solid, fertile, 2 lateral, valve, sterile. Stigmas 'commissural'.

B. *Capsella Bursa-pastoris* (Shepherd's Purse). G 4, 2 median, semi-solid, flat, fertile, 2 lateral, valve, boat-shaped, sterile.

C. *Capsella Bursa-pastoris* var. *Heegeri*. G 4 as in B, but the median pair narrower, the lateral pair wider.

D. *Biscutella*. G 4, 2 median, solid, sterile, 2 lateral, valve, fertile.

E. *Lunaria biennis* (Honesty). G 4, 2 median, semi-solid, boat-shaped, fertile, 2 valve, flat, sterile.

F. *Bunias orientalis*. A 'key' genus. G 4, 2 median, fertile, 2 lateral, sterile, both pairs flat and of the same size.

FIGURE 45.

N.B.—For additional Figures illustrating the construction of the crucifer gynoecium not contained in the literature cited in the present volume on pp. 135–137, see *American Journal of Botany*, Vol. XVI, No. 2, pp. 124 and 136, 1929.

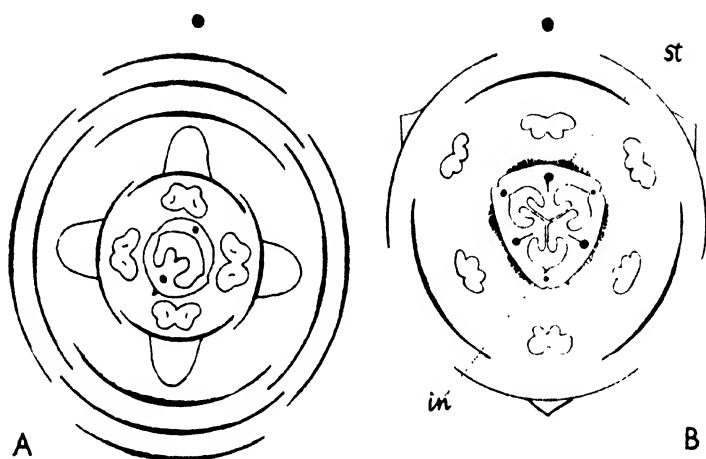


FIGURE 46.

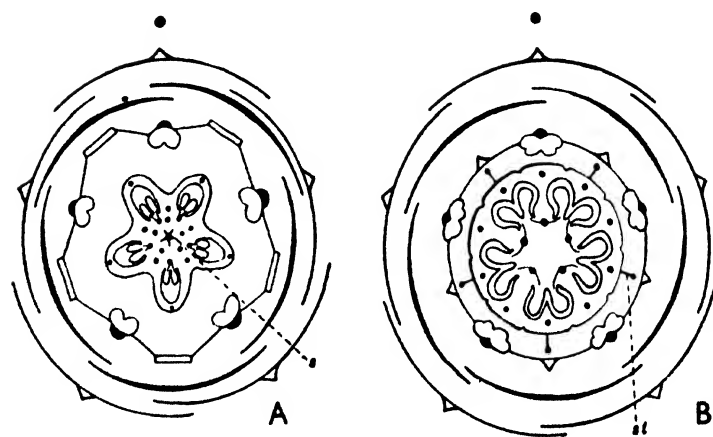


FIGURE 47.

FIG. 46. Berberidaceae and Liliaceae. (Diagrams reproduced (A) and improved (B) from 16, pp. 106 and 110.)

A. *Epimedium alpinum*. G 2, 1 valve, sterile, styleless, 1 semi-solid, fertile, with style and stigma ('commissural').

B. *Tulipa Gesneriana* (Garden Tulp). G 6, 3 solid, sterile + 3 semi-solid, fertile, with sessile stigmas ('commissural'). On the inner face of the wall of the ovary and in line with each sterile carpel midrib is an indentation indicating the line of contact of the two neighbouring semi-solid carpels which have met over the inner face of the intervening sterile carpel but have not coalesced. Sterile carpel midribs unbranched. Fertile carpel midribs with branches which run to the placentae.

*in* indentation, *st* stigma.

FIG. 47. Geraniaceae and Linaceae. (Diagrams reproduced from 16, p. 112.)

A. *Erodium cicutarium* (Stork's Bill). G 5 valve, fertile with midrib and functional placental bundles + 5 solid, sterile with midrib and non-functional placental bundles. *s* stigma rays.

B. *Linum usitatissimum* (Flax). G 5 sterile, forming complete septa at the base of the ovary but at the higher level here shown withdrawn from the centre and projecting only slightly into the loculi, styled, with midrib but without placental bundles + 5 fertile, forming complete septa, styleless, with midrib and placental bundles. *st* style.

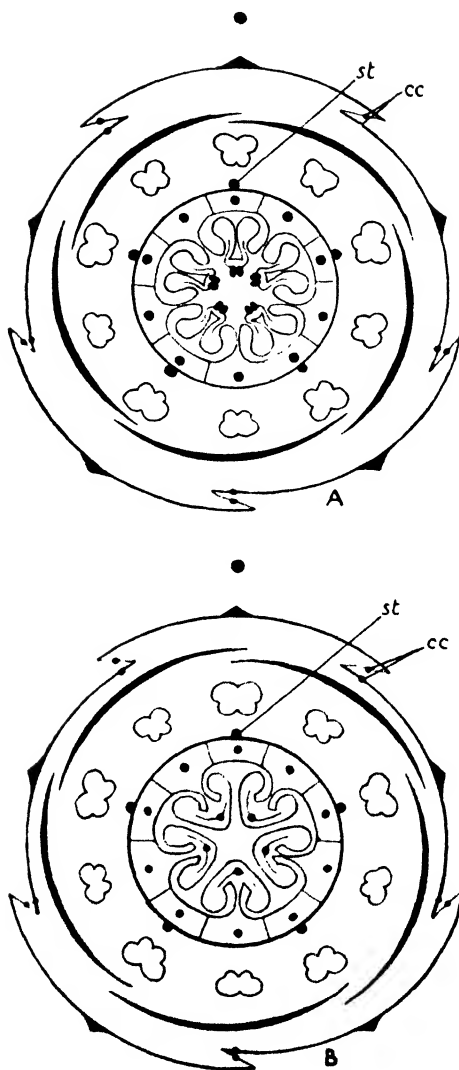


FIGURE 48 A, B.

FIG. 48 A, B. Caryophyllaceæ (17, p. 261, Diagrams A, B improved).

*Lychnis cæli-rosa* an isomerous pentamerous type (K 5 C 5 A 5 + 5 G 5, sterile + 5, fertile) with gynophore. Sterile carpels antesepalous.

A. From the lower region of the flower where the fertile carpels are continuous with the central parenchyma of the axis and form complete septa. At this level the twin placental vascular bundles of each fertile carpel lie so far apart that the adjacent bundles of two neighbouring carpels are closely approximated and simulate a true pair.

B. From a higher level where the central parenchyma has come to an end, the fertile carpels are free on their inner face and the ovary is unilocular. At this level the twin placental bundles of each fertile carpel have converged and fused into a single strand. (For further details see 3, pp. 142, 143†; 9, pp. 190-192†, 17, pp. 239-261†.)

*c c* commissural marginal veins, *st* stigma.

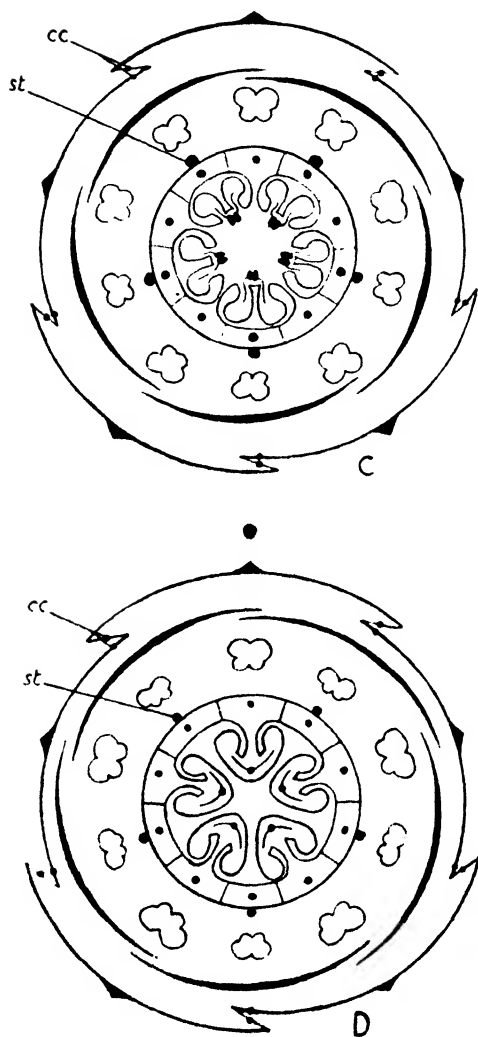


FIGURE 48 C, D.



FIG. 48 C, D. Caryophyllaceæ (*continued*) (17, p. 261, Diagrams C, D improved).

*Agrostemma Githago*, an isomerous pentamerous type (K 5 C 5 A 5 + 5 G 5, sterile + 5, fertile) without gynophore. Sterile carpels antepetalous.

C. From a level corresponding with that shown in Fig. 39 A.

D. From a level corresponding with that shown in Fig. 39 B. (For further details see legend to Fig. 43, A, B.)

*c c* commissural marginal veins, *st* stigma.



# INDEX

OF

## Names of Families and their sub-divisions, Genera and Species

English names are in italics.

The names Angiosperms, Monocotyledons and Dicotyledons are only listed when text accompanies the citation.

Figures in text are indicated by †, Floral Diagrams by ‡.

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# APPENDIX

## A CENTURY'S CHALLENGE TO ORTHODOXY IN TEN CHAPTERS WITH PREFACE AND EPILOGUE

by  
E. R. Saunders

Exhibit in Section K (Botany) at the meeting of  
the British Association for the Advancement  
of Science, Cambridge, August, 1938



## PREFACE

### FLORAL ARRANGEMENT

1829 BRAUN, AL., and SCHIMPER, K. F.

'The regular alternation of cyclic whorls must be accepted.'

Braun and Schimper's conclusion is cited by K. Schumann in *Blüthen-morphologische Studien, Pringsheim's Jahrb. f. wissenschaftliche Botanik*, 20, 1889, p. 360, as follows:

'Von den Begründern der deutschen morphologischen Schule von Braun und Schimper wurde bekanntlich das Theorem aufgestellt dass in einer Blüthe die regelmässige Alternanz der Cyclenglieder angenommen werden müsse.'

1875 EICHLER, A. W.

'So general is this rule (of alternating whorls) that I cannot consider as explained flowers in which superposed whorls are accepted.'

*Blüthendiagramme*, Vol. 1, p. 11.

'So allgemein in der That ist jene Regel, dass ich eine Blüthe, in der noch superponirte Quirle angenommen werden, nicht für erklärt halten kann.'

### CHAPTERS IN THE HISTORY OF THE CARPEL

#### CHAPTER I

1823 LESTIBOUDOIS, T.

'I do not believe that the edges of the valves (of the siliqua) turn in to form the septum.'

*Mémoire sur les Fruits siliquaux*, p. 6:

'Non, je ne crois pas que les bords des valves se portent à l'intérieur pour constituer la cloison.'

#### CHAPTER II

1828 LINDLEY, J.

concluded from the position of the stigmas (*e.g.* in Wall-flower) and the mode of dehiscence of the fruit that the pericarpium was 'formed of four confluent pistilla (carpels) of which two are placentiferous and furnished with stigmata, and two destitute of placentæ and stigmata, but separable in the form of valves.'

*Botanical Register*, Vol. 14 (= Vol. 1 of 2nd Series). See concluding paragraph accompanying Pl. 1168 (*Eschscholzia californica*).

1831-33 KUNTH, K. S.

Put forward the same view as Lindley.

*Handbuch der Botanik*.

*Also Ueber die Blüthen- und Fruchtbildung der Cruciferen.*

## CHAPTER III

## 1840 BROWN, ROBERT

Dismissed the interpretation of the gynæceum of the Cruciferae put forward by *Lindley* and *Kunth* which offered a satisfactory explanation of the 'commissural' stigma based on certain facts, and adhered to the morphological fiction then current.

Horsfield's *Plantae Javanicae rariores*, Part II.

Note p. 108 in the article on 'The relative position of the divisions of the stigma and parietal placentæ in the compound ovarium of plants' contributed by Robert Brown.

This article is reprinted in *Miscellaneous Botanical Works of Robert Brown*, Vol. I, pp. 555-563, published by the Ray Society (1866).

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*Result.* The fiction was retained.

## CHAPTER IV

## 1830 BAUER, FR.

suggested that the presence of 6 vascular bundles in the Orchid ovary and the splitting of the fruit into 6 pieces indicated the presence of 6 carpels (*not* 3).

*Illustrations of Orchidaceous Plants with Notes and Prefatory Remarks*, by J. Lindley, 1830-38.

## 1831 BROWN, ROBERT

rejected Bauer's conclusion, holding the number of vascular bundles and of the segments of the fruit to be without significance in this respect.

*On the Organs and Mode of Fecundation in Orchidæ and Asclepiadæ*, 1831.

Reprinted in *Transactions of the Linnean Society*, Vol. 16, pp. 685-745, 1831.

Also in *Miscellaneous Botanical Works of Robert Brown*, Vol. 1, pp. 489-543, published by the Ray Society (1866).

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*Result.* Current opinion remained unchanged.

## CHAPTER V

## 1834 MORREN, C., and DECAISNE, J.

In view of the two opposite furrows in the ovary of *Epimedium* (Berberidaceæ) suggested that the ovary was composed of 2 carpels (*not* 1), the larger bearing ovules *on the midrib bundle*.

*Annales des Sciences, Botanique*, 2nd Series, Vol. 2, p. 358.

(Observations sur la Flore du Japon suivies de la monographie du genre *Epimedium*.)

## 1861-62 BAILLON, H.

rejected this interpretation, holding that 'the furrows, though vertical, represented a transverse articulation of the carpellary leaf such as may occur in the cauline leaf.'

*Adansonia*, Vol. 2, pp. 268, 275-276.

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*Result.* Morren and Decaisne's true interpretation was ignored and current opinion remained unchanged.

## CHAPTER VI

## 1857 PAYER, J. B.

suggested in Malvaceæ-Ureneæ which were (and in many text-books still are) described as having twice as many styles as carpels (5 carpels, 10 styles) (1) *that there are in reality 10 carpels present*, of which 5 alone form loculi; the alternate 5 which do not being continuous with the septa; and (2) *that all 10 bear styles*.

*Organogénie*, Vol. I, p. 35; Vol. II, Pl. 7, Figs. 11, 12, 14.

## 1872 BAILLON, H.

accepted Payer's interpretation.

*Histoire des Plantes*, Vol. 4 (Malvaceæ), p. 91, footnote 3. Also English Translation, *The Natural History of Plants*, Vol. 4 (Malvaceæ), p. 94, footnote 5, 1875.

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*Result.* General botanical opinion remained unchanged.

## CHAPTER VII

## 1879 STRASBURGER, E.

described and illustrated the fact that in the apocarpous gynæceum of *Astrocarpus* (Resedaceæ) each ovary, formed of a single folded leaf, contains a single ovule which is seated on the carpel midrib.

*Die Angiospermen u. die Gymnospermen*, pp. 57, 58, and Table 8, Fig. 90.

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*Result.* No general inference was drawn from the position of the ovule and the observation brought no change in current opinion.

## CHAPTER VIII

1887-91 KERNER, A. VON M.

took the view that some ovaries were composed of *two* kinds of carpels (*e.g.* those of Cruciferae, Papaveraceae, Violaceae), *one kind bearing ovules, the other not.*

But Kerner's descriptions were not amplified by generalisations or definitions.

*Pflanzenleben*, II, p. 73. Also English Translation (F. W. Oliver, *The Natural History of Plants*), Vol. 2, p. 75, 1895.

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*Result.* Kerner's views had no effect upon current botanical opinion.

## CHAPTER IX

1894 KLEIN, J.

traced the vascular system in the ovary of the Cruciferae and once more put forward the view that it is constructed of 4 carpels, *not 2.*

'Der Bau der Cruciferenblüthe auf anatomischer Grundlage,' *Berichte d. deut. Bot. Gesellschaft*, Vol. 12, p. 18.

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*Result.* Klein's evidence was disregarded and current botanical opinion remained unchanged.

## CHAPTER X

1923 SAUNDERS, E. R.

'The conception of the dimorphic carpel removes the anomaly of the "false" partition and the "commissural" stigma, and brings into harmony and renders intelligible many facts hitherto unexplained or without significance.'

'A Reversionary Character in the Stock (*Matthiola incana*) and its Significance in regard to the Structure and Evolution of the Gynæcium in the Rhœadales, the Orchidaceae and other Families.' *Annals of Botany*, Vol. 37, p. 463.

## EPILOGUE

1929 The conception of Carpel Polymorphism satisfactorily explains

(a) The whole series of anomalies in the pistil of the Cruciferae.

(b) Accounts for the 'commissural' stigma in general.



- (c) Affords a rational explanation of obdiplostemony.
- (d) Throws a new light on parietal, free-central, superficial and axile placentation.
- (e) Demonstrates that the terminal carpel, the supernumerary style and the false partition are not realities.
- (f) Renders intelligible the sterility of ♂ flowers possessing a reduced female organ.

E. R. Saunders, *Report British Association*, 1929, Section K (Botany).

- 1936 'A study of the vascular ground-plan is essential to a full understanding of the floral ground-plan. The one as much as the other is the outcome of certain inherent rhythmic processes which bring about the orderly and symmetrical disposition of the component units.'

E. R. Saunders, 'On Rhythmic Development and Radial Organisation in the Flower,' *Journal Linnean Society*, Vol. 50, p. 321, 1936.

- 1937 'A satisfactory solution of the Problems of Floral Morphology is not to be expected unless the evidence of external appearance is supplemented by that of internal structure.'

E. R. Saunders, *Floral Morphology*, Vol. I, Introduction, p. 1, 1937.

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